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Cover. Reconstruction of the fertile apex of the lycopod-like plant *Asteroxylon mackiei*, from the Lower Devonian Rhynie Chert, Aberdeenshire, Scotland, × 5. The model was made for the Royal Scottish Museum, Edinburgh, by Joyce Collard of H. R. Studios following a reconstruction by W. G. Chaloner, based on photographs by G. Lyon. The photograph comes from a forthcoming booklet by W. G. Chaloner on early land plants, to be published for the Royal Scottish Museum.

FAUNAL RESPONSE TO THE INSTABILITY OF REEF HABITATS: PLEISTOCENE MOLLUSCAN ASSEMBLAGES OF ALDABRA ATOLL

by JOHN D. TAYLOR

ABSTRACT. Coral ecosystems are considered by many biologists to have been stable over ecological and evolutionary time, yet the Pleistocene history of reefs reveals complex and large-scale habitat changes associated with glacio-eustatic rise and fall of sea-level. Study of the molluscan assemblages from three Pleistocene rock units, together with faunas from Recent habitats on Aldabra Atoll, shows that shallow-water habitats and the associated communities have changed considerably during the period of the late Pleistocene. The communities inhabiting the shallow water of Aldabra today are very different from those of 125 000 years ago, and the latter are in turn different from those of two older Limestones.

Habitat and faunal changes of a similar magnitude are known or can be predicted for many other reefs in the Indo-Pacific province, and it is clear that present-day habitats have been formed and occupied only during approximately the last 3000–5000 years. The high diversity of reef faunas seems to be associated with the long-term survival and stability of the species pool of the Indo-Pacific province and not with the stability of individual reef systems.

CORAL reefs are acknowledged to be amongst the most complex and diverse ecosystems on earth, and hypotheses concerning the high level of tropical diversity stress the stability and predictability of such environments (Pianka 1966; Fischer 1960; Sanders 1968; Pielou 1975). A pervasive view is that coral-reef faunas have evolved in environments that have been stable for considerable periods of time (Newell 1971). Although these ideas are intuitively satisfying there is little information on the relative stability of tropical environments. However, recent studies of the history of individual reef systems have revealed that reef growth does not proceed in an uninterrupted continuous sequence, but that periods of reef accumulation are punctuated by times of non-deposition and erosion (Braithwaite 1973; Mesolella *et al.* 1970; Montaggioni 1974; Purdy 1974; Stoddart 1973, 1976; Ladd *et al.* 1970; Tracey and Ladd 1974). The erosional events occurred during low sea-level stands of the late Pleistocene when reefs were emergent. Successive periods of reef accumulation may be very different in character, reflecting differences in environmental conditions (Braithwaite *et al.* 1973). Furthermore, palaeotemperature analysis of Foraminifera from deep-sea cores has shown that during the Wisconsin glaciation, considerable areas of the tropics which today support prolific reefs would have been too cold for active reef growth (Emiliani 1971; see map in Stoddart 1973).

Clearly, the environmental changes in the tropics induced by the Pleistocene glaciations were not as severe as those of higher latitudes. They nevertheless had profound effects upon the reef environment, although Newell (1971, p. 21) asserts that tropical habitats were scarcely altered during the glaciations. Even though the main outlines of reef history during the late Pleistocene are now beginning to be

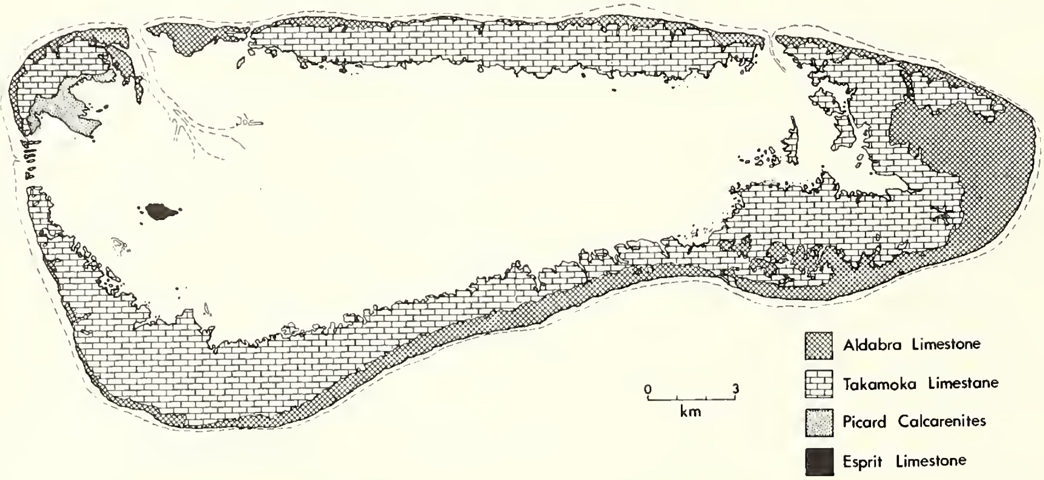
[Palaeontology, Vol. 21, Part 1, 1978, pp. 1–30.]

established (Stoddart 1973) we know very little about the faunal response to these environmental changes.

Recent geological studies at Aldabra Atoll in the Indian Ocean revealed a sequence of three late Pleistocene limestones containing abundant fossil molluscs (Braithwaite *et al.* 1973). This paper describes the molluscan assemblages from these three limestones, and, combined with a brief account of the Recent marine molluscan fauna, gives some insight into the evolution of reef faunas and the response of the molluscan faunas to the changing environmental conditions of the late Pleistocene.

GEOLOGICAL SETTING AND HISTORY OF THE ALDABRA ATOLL

The general structural and geomorphological background to Aldabra has been described by Stoddart *et al.* (1971); the atoll is one of a group of slightly elevated coral islands to the north of Madagascar; they are the subaerial tips of individual seamounts which rise 4000 m from the floor of the Somali Basin. The atoll consists of an annular rim surrounding a shallow lagoon (text-fig. 1); four main islands rise about 8 m above sea-level and vary from 0·25 to 5·0 km in width. The total area of the atoll is about 365 km^2 of which the land occupies 155 km^2.



TEXT-FIG. 1. Geological map of Aldabra Atoll showing the major marine deposits.

The surface geology (text-fig. 1), described by Braithwaite *et al.* (1973), shows a complex series of Pleistocene depositional and erosional events, consisting of alternating shallow-water marine limestones, with limited terrestrial calcarenites, soils, phosphorites, and cavity-fill deposits. The deposits occur in association with, or alternate with, erosional events which produced solutional dissection of the limestones, or marine planation. In the probable absence of tectonic activity, these events must be interpreted in terms of the independent variable which is the glacio-eustatic rise and fall of sea-level.

The stratigraphic relationships of the main deposits on Aldabra are outlined in text-fig. 2. There are three main marine deposits, namely the Esprit, Takamaka, and Aldabra Limestones; they are separated by erosional events, which in the main left no depositional record. Since the deposition of the Aldabra Limestone 125 000 years ago (Thompson and Walton 1972) there has been a progressive, but oscillating, lowering of sea-level to the glacial minimum about 17 000 years ago when sea-level probably stood at about 130 m below the present (Bloom *et al.* 1974; Chappell 1974*b*). Sea-level rose rapidly in post-glacial times and probably reached approximately its present position at about 3000–5000 years ago. We have no evidence of any extensive marine deposits post-dating the Aldabra Limestone. Present-day conditions at Aldabra may in this context be viewed as an erosional event, and information on the present-day fauna might be extrapolated back to interpret what communities may have been present during the long periods for which we have no depositional record.

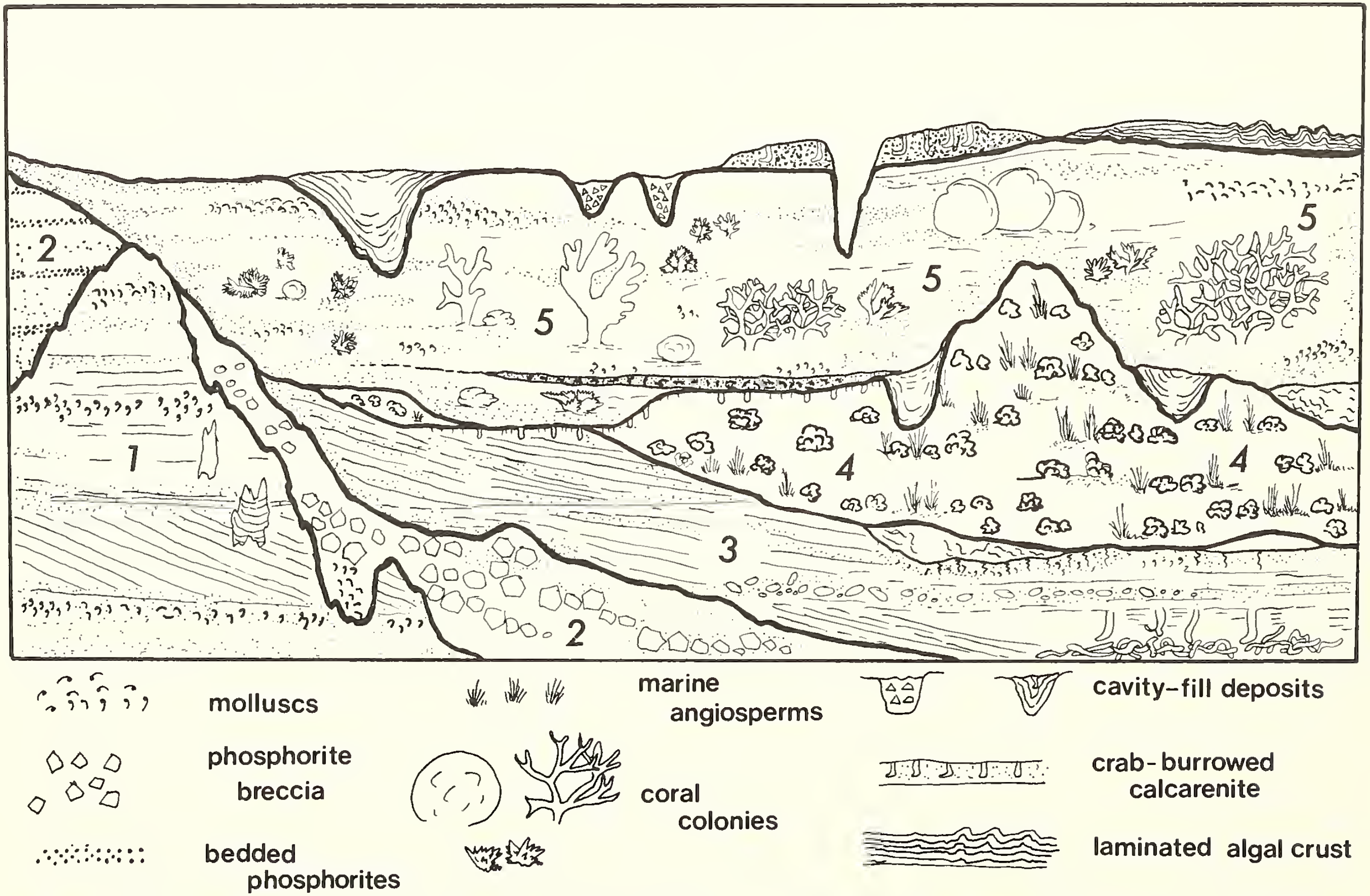
MOLLUSCAN FAUNAS

Most of the material described in this study was collected during the period from June to September 1969 and a small additional quantity in 1973. In all, about 8000 molluscs were collected from eighty-five sampling sites; all the material, together with station lists and grid references is deposited in the Department of Palaeontology, British Museum (Natural History). Full details of species from the various deposits are deposited with the British Library, Boston Spa, Wetherby, Yorkshire, LS23 7BQ, U.K. as Supplementary Publication No. SUP 14009 (12 pages).

Esprit Limestone fauna

These rocks, the oldest on the atoll, are exposed only on the small island of Esprit, situated at the western end of the lagoon (text-fig. 1). They consist of about 8 m of fine-grained calcarenites with the fossils tending to be concentrated into bands about 40 cm thick separated by more or less fossil-free sediment; cross bedding is seen at some levels. The rocks are well cemented and spectacularly dissected by solutional erosion. Unfortunately dissolution of the aragonite skeletons, the extensive fretting of the limestone, and the subsequent partial deposition of phosphate into the moulds and cavities has resulted in poor preservation of a diverse molluscan fauna. The only other fossils of importance are corals which occur at some levels and these are also badly preserved but mainly appear to be small colonies of *Favia* and *Goniastrea*.

The molluscan fauna, although abundant, is so badly preserved that in many cases only generic determination has been possible. Silicone rubber casts were made from many moulds. Twenty-six bivalve and twenty-eight gastropod species (see list in Appendix SUP 14009) have been extracted from the Esprit Limestone. The bivalves are numerically much more important than the gastropods which are represented mostly by single specimens. Of the twenty-six species of bivalves, 65% are burrowers, 20% epifaunal byssate, and 15% free-living members of the epifauna. The burrowers are numerically by far the most important element, comprising 88% of all individuals. The most important species are *Glycymeris* sp. (possibly *tenuicostatus*), *Fragum fragum*, and *Trachycardium* sp. which are all shallow-burrowing suspension feeders; also common are the deeper-burrowing suspension feeders *Dosinia* (*exilium* and



TEXT-FIG. 2. Stratigraphic model for the exposed Pleistocene rocks of Aldabra showing the general relationships of the rock units. 1, Esprit Limestone (marine). 2, Esprit Phosphorites (non-marine). 3, Picard Calcarenites (non-marine). 4, Takamaka Limestone (marine). 5, Aldabra Limestone (marine). The other discontinuous rock units shown, are minor, mainly non-marine deposits. Vertical scale about 9 m, horizontal scale 10 km.

nanus). Only four species of deposit feeders were found, *Tellinella* being the most abundant. The epifaunal species are all uncommon and their presence must have depended upon the availability of suitable attachment sites which, except for the occasional corals, were rare in these deposits. Some of the species found, *Hippopus hippopus* and *Chlamys* species, could live freely upon the sediment surface.

The gastropods are mostly uncommon, and of the twenty-eight species recorded, 71% are normally associated with soft substrates, either as burrowers or surface dwellers, 21% with hard substrates, and 7% parasitic or commensal. In terms of feeding categories 57% of species are algal or detritus feeders, 25% are active carnivores, 7% faunal grazers, and 11% other categories such as suspension feeders, scavengers, or parasites. Various species of *Cerithium*, *Strombus*, and *Terebellum terebellum* are the most common elements; other species are mainly represented by single records.

The assemblage of molluscs is predominantly a soft substrate fauna with only minor contribution from epifaunal hard-substrate species. The fauna inhabited a well-sorted sediment relatively free of organic detritus, but possibly with a surface algal mat and some larger algae, but apparently not *Halimeda* (frequently common in this type of habitat). Several indicator species suggest that for much of the rock sequence the water depth at the time of deposition was probably about 5–20 m; but higher in the rock sequence the presence of abundant *Cerithidea*, a gastropod found living today on the trunks of mangroves, and also the mangrove-associated species *Terebralia palustris* and *Cerithium morum*, indicate a shallowing of the water to intertidal conditions.

The fauna can thus be interpreted as inhabiting a quiet lagoon from 5 to 20 m deep, which in time shallowed, perhaps as a result of sedimentation or falling sea-level and was colonized by mangroves. It must be emphasized that the exposed rocks represent only a tiny fraction of the total area of the atoll, and evidence of the general environmental framework is lacking.

The Takamaka Limestone

This rock unit, characterized by an abundance of calcareous red algae, is about 3 m in thickness and is exposed over wide areas of the atoll (text-fig. 1). There is little facies variation over the entire extent of the atoll, and the rock consists basically of abundant calcareous red algae, the most common genera being *Lithophyllum*, *Mesophyllum*, and *Lithothamnion*.

These occur as profuse papillate heads, foliose masses, and encrusting sheets, which in some places form constructional frameworks. Corals are locally fairly common but only a few species occur of the genera *Tubipora*, *Favia*, *Platygyra*, *Seriatopora*, *Acropora*, *Goniastrea*, *Porites*, and *Millepora*. The rock matrix is usually a white sediment which varies in grain size from a calcareous mud to calcarenite; moulds of *Halimeda* segments and *Seriatopora* branches are abundant in the muds. Facies variations which do occur involve changes in the abundance of the calcareous algae and corals and in the grain size of the matrix. The main area of facies variation is at the eastern end of the present lagoon where the lithothamnoid algae are less common; the matrix varies between a calcilutite and calcarenite and contains mainly branching corals, particularly *Porites nigrescens*.

The Takamaka Limestone is severely dissected by solutional erosion, and the textural relations of the rocks are frequently obscured. There has been a complex post-depositional diagenetic history involving the several phases of solutional erosion and not surprisingly the fossils are generally badly preserved. The corals are usually completely recrystallized, and amongst the molluscs the aragonitic species have been completely dissolved away, leaving moulds. Silicone rubber casts were made from these moulds.

Molluscan fauna. Molluscan diversity and abundance in this deposit is usually rather low. Collections were made at twenty-three sites, but at many localities no mollusca were found. At the western end of the atoll, molluscs are generally rare or uncommon but in the east the fauna is rather more diverse and numerous. The higher diversity in the east may be associated with the facies changes mentioned above.

Twenty-four species of bivalves were found; 58% are epifaunal, either byssate, cemented or free living; 42% are burrowers and well over half of these are suspension feeders. Most of the burrowing species, including *Ctena fibula*, *Pinguitellina robusta*, *Scissulina dispar*, and *Dosinia* occur at one or two sites at the eastern end of the present lagoon where calcarenites are more extensive. The more usual situation over most of the rest of the Takamaka Limestone exposure is the presence of one or two byssate nestling species such as *Cardita variegata* or *Barbatia* or the large *Tridacna maxima* and *T. gigas*.

Gastropods are numerically much more important and thirty-two species have been found of which 65% are epifaunal species normally associated with hard substrates, 18% live epifaunally upon soft substrates, and a further 17% are probably burrowers. In terms of feeding categories, 46% are algal feeders, 31% predators, 15% faunal grazers, and 6% scavengers. Most of the species are uncommon, and the characteristic feature of the fauna is the numerical dominance of Archaeogastropoda which comprise 66% of individuals with *Trochus maculatus*, *T. radiatus*, *Tectus mauritianus*, *Clanculus* cf. *limbatus*, *Phasianella*, *Acmaea*, and *Haliotis varia* particularly common. The only other common gastropods are *Cypraea helvola* and several species of *Cerithium*.

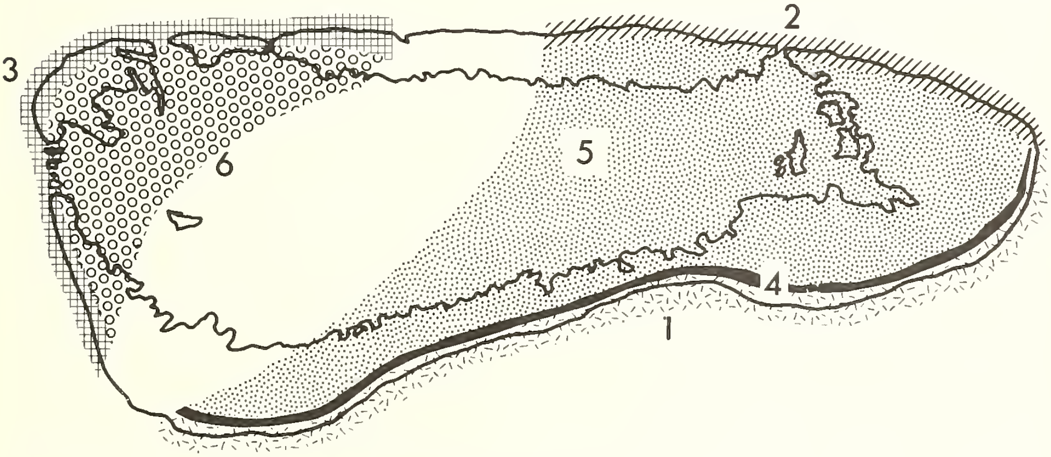
The environmental conditions represented by the Takamaka Limestone are not easily interpreted. On the one hand the abundance of calcareous red algae usually indicates well-circulated, shallow, water; whilst, on the other hand, the abundance of fine-grained sediment indicates a quiet depositional environment. The widespread occurrence of the facies and the low diversity of the fauna are problematic. Braithwaite *et al.* (1973) have interpreted the Takamaka Limestone as representing an environment of meadows of the marine angiosperm *Thalassodendron ciliatum* which frequently colonizes hard substrate areas; calcareous red algae and *Halimeda* are abundant beneath the leaf canopy and fine sediment accumulates in the interstices. Both molluscan and coral diversity are usually fairly low in these habitats. Large stands of *Thalassodendron* growth exist on various shallow banks of the western Indian Ocean and on parts of the east African mainland.

Some of the molluscs from the Takamaka Limestone support this interpretation; for example, *Phasianella*, one of the most abundant gastropods, is today often found living on the leaves of *Thalassodendron*, and other Trochacea are frequently observed around the stem bases and among the underlying calcareous algae. Davies (1970) has described comparable *Posidonia*/calcareous algae communities from Shark Bay, West Australia, in which trochid gastropods, *Phasianella*, *Cerithium*, and a few byssate bivalves such as *Cardita* are common.

The Aldabra Limestone

This extensively exposed limestone (text-fig. 1) is much the best preserved of the marine depositional events; it was formed about 125 000 years ago and consists basically of a 6–8 m thick calcarenite containing abundant corals and molluscs. Limestones of similar age representing a sea-level of up to 10 m above the present, have been recorded from widely separated parts of the tropics (Bloom *et al.* 1974; Chappell 1974*a*).

Braithwaite *et al.* (1973) have shown that the Aldabra Limestone was deposited in shallow water, probably not more than 10 m deep, covering a broad annular platform formed from the erosion of the underlying Takamaka Limestone. The sediment complex which built up on this platform consisted of coral pinnacles and knolls concentrated around the atoll rim and rising from a generally sandy floor. For probably most of the depositional period, there was no land present, and Aldabra consisted of a submerged, shallow, coral-covered bank. Early in the deposition of the limestone a prominent bedding plane and a thin deposit may mark a temporary emergence.



TEXT-FIG. 3. Reconstruction of the distribution of the main facies of the Aldabra Limestone. 1, *Acropora humilis* facies. 2, *Acropora palifera* facies. 3, Faviid-dominated facies. 4, *Goniastrea* facies. 5, *Halimeda* sands facies. 6, *Porites*-coral-knoll facies.

Several distinct biofacies have been recognized on the basis of coral associations and sediments (text-fig. 3) which represent changes in hydrodynamic conditions around and across the atoll. An estimated maximum of about 400 m of Aldabra Limestone has been removed by erosion from around the atoll rim. An abundant and diverse molluscan fauna comprising over 300 species has been recovered from the Aldabra Limestone; the preservation varies from excellent to poor depending upon the local diagenetic history.

The major biofacies recognized by Braithwaite *et al.* (1973) have been used as a framework for the description of the molluscan assemblages, and collection samples have been grouped according to their location within the facies boundaries (full details of species, abundance, and facies deposited in British Library SUP 14009). The relative abundance of the major taxa (text-figs. 3, 4) were obtained by combining all the data from collection sites within each facies. Except for single records, the number of bivalve shells found were halved.

1. *Acropora humilis-dominated facies.* Along 20 km of the southerly and easterly shores of the atoll, the main facies of the Aldabra Limestone consists of a *Halimeda*-rich calcarenite separating patches of more or less abundant coral. The corals are dominantly species of *Acropora*, particularly corymbose *A. humilis* and spray-like branched forms, although the stagshorn form *A. formosa* and *A. palifera* are common. Other corals present include *Pocillopora eydouxi*, *Goniastrea*, *Favia*, *Fungia*, *Galaxea*, *Hydnophora*, *Goniopora*, and sometimes massive *Porites* towards the base of the limestone. Areas of solid constructional frame growth are uncommon, and in some places the corals are tumbled.

Compared with other sites the molluscan fauna is very sparse. The dominant gastropod is the large thick-shelled *Turbo argyrostomus*, which with the other trochaeans *Tectus mauritianus* and *Trochus maculatus*, comprise 55% of the fauna. The Cypraeidae form 16% of the fauna with *Cypraea helvola*, *C. cicercula*, and *C. nucleus* as the most common species. Other common species normally associated with hard substrates are *Columbella turturina*, *Drupella cornus*, *Magilus*, *Conus sponsalis*, and *Neritopsis radula.* A few species, namely *Cerithium echinatum*, *Rhinoclavis asper*, and *Polynices tumida*, are characteristic of soft substrates and would have inhabited the sand between the corals. Bivalves are not abundant, and a rather sparse fauna was extracted from this facies. The byssate *Barbatia fusca*, typical today of *Acropora*-dominated habitats, is the most abundant species accounting for 33% of individuals; the burrowing tellinaceans, *Scissulina*, *Pinguitellina*, and *Scutarcopagia*, make up a further 24% of individuals whilst the byssate *Tridacna maxima* is the only other common bivalve. The large *T. gigas* is occasionally found in the *Halimeda* sands.

2. *Acropora palifera-dominated facies.* To the north and east of the atoll the coral fauna consists dominantly of large colonies of *Acropora palifera* with large clubby branches up to 3 m high; stagshorn *Acropora*, *Favia*, *Goniastrea*, and *Galaxea* together with occasional massive *Porites* also occur. Over most of its development this facies consists of scattered coral colonies in a *Halimeda*-rich calcarenite to calcirudite matrix, and only high in the rock sequence is there any development of constructional frames.

The molluscan fauna is similar but rather more diverse than facies 1, *Turbo argyrostomus* again being the most abundant gastropod with the other trochaceans *Tectus mauritianus* and *Trochus maculatus* also fairly common and together comprising about 56% of the fauna. Cypraeidae are abundant and diverse, and eighteen species account for a further 11% of gastropod numbers. The Conidae (11%), Cerithiacea, mainly *Cerithium echinatum* (7%), and *Strombus* (3%) are the other abundant taxa. Bivalves are uncommon, and again the most abundant species is *Barbatia fusca* (60% of individuals) with *Tridacna maxima* (18%) and a variety of other byssate or cemented bivalves such as *Trapezium*, *Spondylus*, *Chama*, and *Plicatula* making up the rest of the fauna.

3. *Faviid coral-dominated facies.* This biofacies, found around the western and north-western parts of the atoll, consists of pinnacles of often prolific coral growth which are separated by areas of coarse calcarenite made up largely of coral, algal, and molluscan debris. The coral fauna consists dominantly of genera with rounded to massive growth forms such as *Favia*, *Platygyra*, *Leptoria*, *Symphyllia*, or *Porites*. However, branching forms such as *Pocillopora*, *Acropora palifera*, *A. humilis*, *A. formosa*, and *Millepora* are present and sometimes abundant. At some sites there are growths of rigid-frame structures with the faunal composition suggesting shallow-water, high-energy conditions.

This is the richest and most diverse of the atoll-edge facies, containing about twice as many species as facies 1 at the south-eastern end. The molluscan fauna is again overwhelmingly dominated by archaeogastropods of the superfamily Trochacea and in particular by *Turbo argyrostomus*, *Trochus*, and *Clanculus* which make up 70% of gastropods found. The Cypraeacea are represented by fifteen species which make up 10% of the fauna with *Cypraea helvola*, *C. cicercula*, *C. nucleus*, and *C. staphylaea* the most common. The two related families of Muricidae and Coralliophilidae are represented by six species of which *Drupella cornus*, *Coralliophila violacea*, and *Magilus*, which feed upon or are associated closely with living coral (Robertson 1970) are abundant. *Columbella turturina* (Columbellidae 4%) and *Peristernia nassatula* (Fasciolaridae 2%) are other common species normally associated with hard substrates. Some forms, such as *Cerithium echiatum*, *Olivella*, *Harpa*, and *Terebra*, are typical of soft substrates and would have lived in the sediment pockets between the coral knolls.

The bivalve fauna is again dominated by *Barbatia fusca* (Arcacea 41%); other byssate forms include *Chlamys cuneolus* (Pectinacea 6%), *Trapezium* (Arcticacea 7%), and *Tridacna*. Burrowing bivalves present are mainly the opportunistic tellinacean *Scutarcopagia scobinata* which can inhabit small and ephemeral sand pockets between corals.

4. *Goniastrea-dominated facies.* Immediately inside the *Acropora*-dominated outer facies along the south and east sides of the atoll there is a belt about 150 m wide where rounded colonies of *Goniastrea* up to about 1 m in diameter are the dominant coral; other corals are subordinate but include species of *Acropora*, *Millepora*, *Hydnophora*, *Favia*, and *Platygyra*. The sediment between the corals is a *Halimeda*-rich calcarenite. Only a small mollusc fauna has been obtained from this the least diverse of any of the facies; this low abundance is a real feature rather than collection failure. *Turbo argyrostomus* is again the dominant mollusc, comprising about 35% of individuals collected, with several species of *Cypraea*, particularly *C. helvola; Rhinoclavis asper*, *Cerithium echinatum*, *Columbella turturina*, and *Drupella cornus* are the only other common gastropods.

Bivalves are very sparse, the most abundant forms being species of *Chama* (40% of the fauna) with Arcacea, Veneracea, Lucinacea, and Tridacnacea comprising about 10% each of the rest of the sample.

5. *Halimeda sands facies.* A broad area of the south-eastern corner of the atoll consists of fairly open *Halimeda*-rich calcarenites with more or less isolated coral colonies, of a limited number of species, and small, more diverse, coral patches. The main corals present are *Goniastrea*, *Acropora palifera*, *A. formosa*, massive *Porites*, *Goniopora*, and *Millepora*. Other forms such as corymbose *Acropora*, *Hydnophora*, and faviids occur in the small patches.

The dominant element in the gastropod fauna is the Cerithiacea, comprising 36% of individuals; the most abundant species are the sand-living *Rhinoclavis asper* and *Cerithium echinatum*, although seven other species are present. Other gastropods characteristic of soft substrates include *Strombus gibberulus* (7%), *Polynices tumida*, and species of *Nassarius*, *Conus*, and *Terebra*. Gastropods normally associated with hard substrates and probably inhabiting the coral patches include the Cypraeidae, with sixteen species forming 15% of the fauna, the Muricidae, particularly *Drupella cornus*, and *Columbella turturina* of the Columbellidae (9%).

The most abundant bivalves are species of *Tridacna* with *T. crocea* found in excavations eroded into the underlying Takamaka Limestone, and with large *T. gigas* free-living in the *Halimeda* calcarenites and *T. maxima* associated with the coral patches. Most of the other bivalves are burrowing species from the sands and include *Codakia punctata*, *Ctena*, *Jactellina clathrata*, *Scissulina dispar*, *Scutarcopagia scobinata*, and *Timoclea*. Small remanié deposits of Aldabra Limestone on small islets in the south central lagoon have yielded a slightly different fauna and are shown separately in text-fig. 4. Coral colonies of *Acropora*, *Pocillopora*, *Seriatopora*, *Favia*, and *Goniastrea* are separated by a *Halimeda*-rich calcarenite. *Polynices tumidus* is the dominant gastropod (Naticidae 23%), with *Cerithium echinatum* (Cerithiacea 16%), *Strombus gibberulus*, *Trochus maculatus*, *Cypraea helvola*, and *Conus* species also common. The most abundant bivalve is *Fragum fragum* (Cardiacea 30%), and *Chama* species (23%) with *Timoclea marica* (Veneracea 6%), *Ctena*, *Scissulina dispar*, and *Tridacna maxima* also common.

6. *Porites coral-knoll facies.* Occupying a wide area of the north-west quadrant of the atoll there is a facies consisting of coral knolls separated by patches of sand and coral debris. The knolls vary in coral composition; many in the northern part consist basically of *Porites* colonies, but many other corals may occur, particularly branching *P. nigrescens*, large *Acropora palifera*, corymbose *Acropora*, *Favia*, *Platygyra*, and *Galaxea*; *Seriatopora* and *Fungia* are common in the sands around the knolls. One patch at Polymnie consists of broad, flat, cone-shaped colonies of *A. hyacinthus*. The intervening areas between the knolls is uniform sands or coarse rubble and debris; *Halimeda* segments are usually subordinate in these sediments, which at some sites are made up almost entirely of shell debris.

This is by far the most diverse facies in terms of species diversity and numerical abundance of molluscs, and 137 gastropod and 60 bivalve species have been recovered from a sample of 2586 molluscs. The dominant gastropod families represented are the Cerithidae and the Cypraeidae, comprising 25% and 21% of individuals respectively. The ten cerithiid species are all characteristic of soft substrates with *Rhinoclavis asper* and *Cerithium echinatum* the dominant forms. A few other soft substrate gastropods are common, including *Strombus gibberulus*, *Polynices tumidus*, nine species of

Terebra, and seven of *Nassarius*. The Cypraeidae are the most diverse family with twenty-one species recorded from this facies, all of them characteristic of hard substrates; *Cypraea fimbriata*, *C. helvola*, *C. scurra*, *C. isabella*, and *C. caurica* are the most abundant species. Other important gastropods which prefer hard substrate habitats are *Tectus mauritianus*, *Columbella turturina*, *Peristernia nassatula*, *Cantharus undosus*, and the coral-feeding *Drupella cornus* and *Coralliophila violacea*.

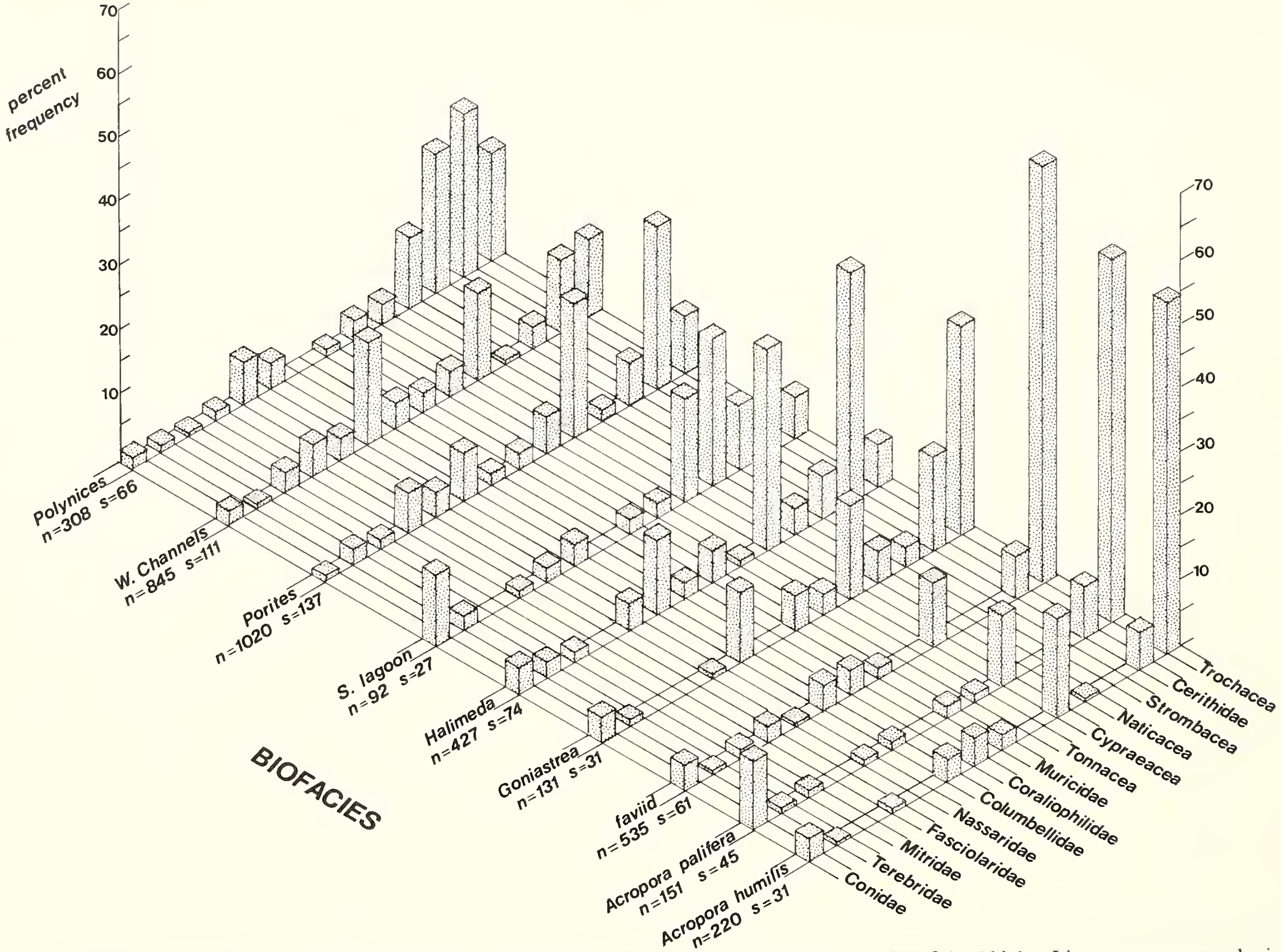
By far the most abundant bivalve superfamily is the Arcacea, constituting 34% of individuals found, with *Barbatia fusca* once again the most abundant species, but *B. helblingi* and *B. tenella* are also common. The burrowing Tellinacea are the next most abundant group with *Pinguitellina robusta*, *Scissulina dispar*, *Jactellina clathrata*, and *Semele jukesi* as the most common species. The Veneracea, another burrowing group, are the next most important, the most abundant species being *Pitar obliquata*, *Timoclea marica*, and *Amiantis grata*.

There is a considerable amount of variation in faunal composition between samples in this facies depending upon the amount of coral present in the habitat. Samples in the Camp Frigate–Passe Gionnet area contained a high proportion of soft substrate species. The site on Polymnie dominated by *Acropora hyacinthus* yielded a high abundance of the cemented bivalves *Chama*, *Spondylus*, and *Ostrea*. In the West Channels area the Aldabra Limestone is extremely fossiliferous; a very large sample was obtained from this area and this is shown separately in text-figs. 4 and 5; the fauna is similar in general to the rest of the *Porites*-knoll facies with the Cerithidae, Cypraeidae, Columbellidae, and Fasciolaridae among the dominant groups.

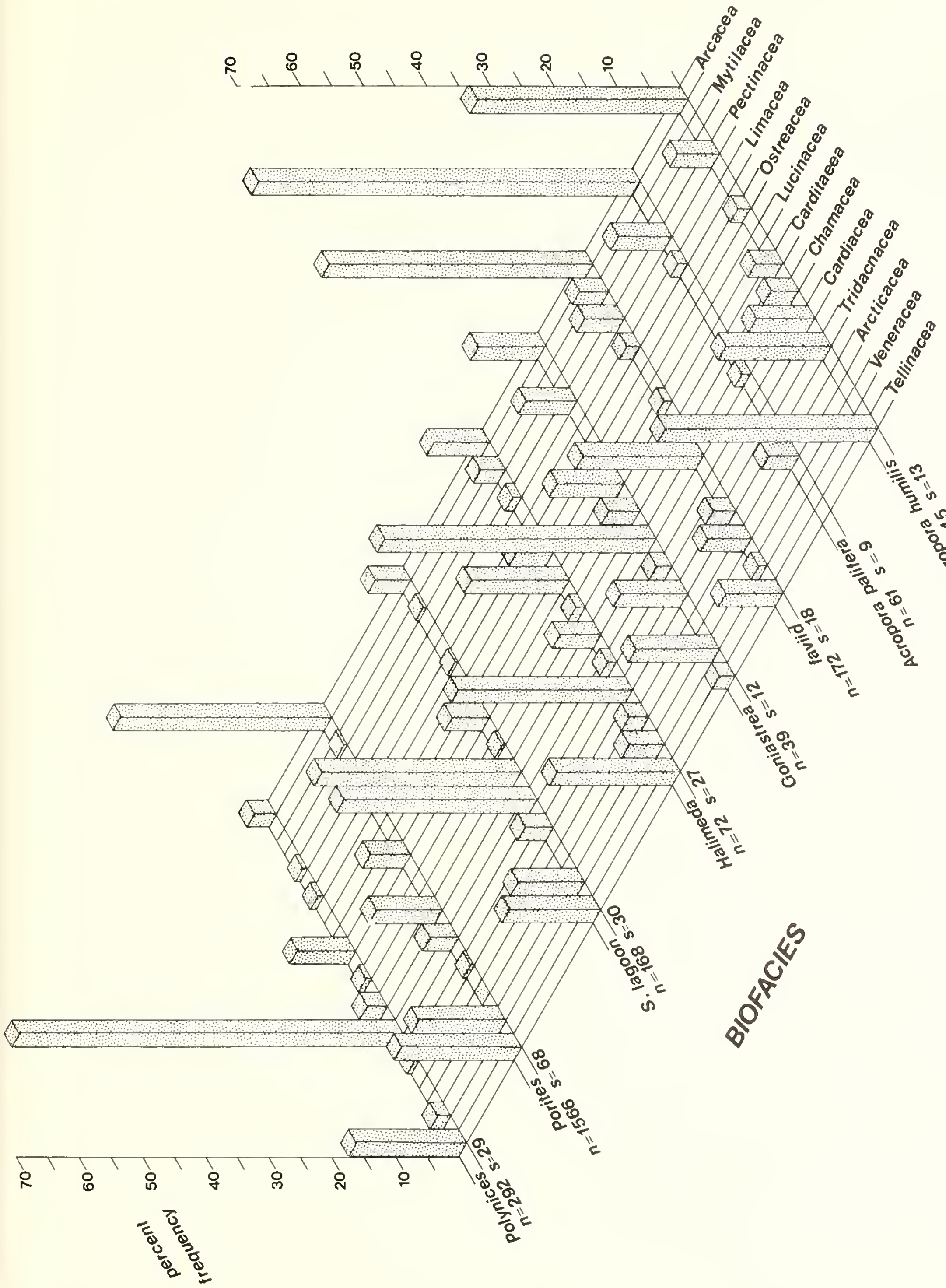
7. *Polynices-Fragum facies*. This is a distinctive thin deposit present over large areas of the south-eastern corner of the atoll; it represents a distinct phase within the lower part of the Aldabra Limestone sequence. The 10–15 cm thick hard, well-cemented calcarenite sometimes lies above a clionid sponge-bored surface of fibrous crusts of possible subaerial origin. The calcarenite contains rolled, algally coated coral fragments, *Halimeda* segments, and the foraminiferan *Marginopora*.

Molluscs are common and well preserved, most of them being species normally associated with soft substrates. The most abundant taxon is the Cerithidae with 26% of individuals, consisting mainly of one species, *Rhinoclavis asper*. Other important gastropods are *Strombus gibberulus* (Strombidae 21%) and *Polynices tumidus* (Naticidae 11%). The Trochacea constitute 17% of the fauna comprising mainly *Cantharidus*, *Phasianella*, and *Tectus mauritianus*. *Nassarius arcularis*, *N. echinata*, *N. pullus*, and *N. albescens* comprise 7% of the fauna.

The bivalve fauna is dominated by the shallow-burrowing cardiid *Fragum fragum* (60%) with tellinaceans, mainly *Scissulina dispar*, *Jactellina clathrata* (17·5%), and Lucinidae, mainly species of *Codakia* and *Ctena* (9%). In some places the most abundant molluscs in this bed are *Codakia*, *Phasianella*, *Bulla*, *Scissulina*, *Cantharidus*, and *Strombus gibberulus*; these genera are today often associated with beds of marine angiosperms such as *Thalassia*, *Cymodacea*, and *Thalassodendron* (Taylor 1968, 1971*a*). At other localities the fauna is dominated by *Fragum fragum*, *Polynices*, and *Rhinoclavis asper*, and these species are usually found at the present day in unvegetated but shallow sand patches. Salvat (1972) shows that in Réao lagoon, *F. fragum* is found only in water less than about 2·5 m deep. The environmental interpretation of



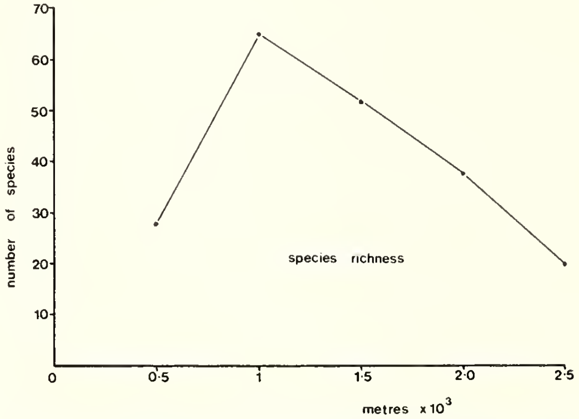
TEXT-FIG. 4. Relative abundance of the major gastropod families and superfamilies in the various facies of the Aldabra Limestone. n = sample size; s = number of species.



TEXT-FIG. 5. Relative abundance of bivalve superfamilies in the various facies of the Aldabra Limestone. n = sample size; s = number of species.

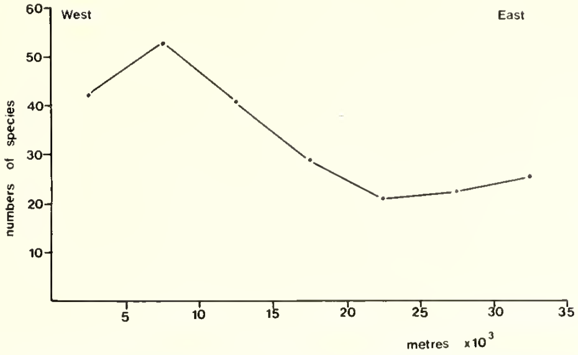
the Aldabra fauna is that it represents intertidal, or shallow sublittoral, marine grass and open sandy habitats, which may have been the first sediments deposited after a temporary emergence represented by the fibrous crusts (Braithwaite 1975).

Summary of the Aldabra Limestone fauna. Around the atoll rim the molluscan fauna varies greatly in abundance and species richness, from the richest area of the *Favia* facies of the north-west to the species-poor areas of the *Acropora* and *Goniastrea*-dominated facies of the south-east. Although three major biofacies around the atoll rim are recognized on the basis of sedimentological and coral features, the species composition of the molluscan fauna is essentially similar around the atoll, being dominated by *Turbo argyrostomus*, *Trochus*, and *Barbatia fusca*, with other hard substrate forms such as *Columbella turturina*, *Drupella cornus*, *Coralliophila*, and *Cypraea* spp. abundant. The main distinctions of the molluscan faunas are seen between the outer and inner facies. The numbers of Trochacea and Arcacea decline markedly inwards with a complementary increase in the importance of Cerithidae, Strombidae, Tellinidae, and Veneridae. The distance from the atoll edge thus seems to be an important parameter determining the composition of the fauna; this radial distance, of course, reflects a complex interaction of many environmental changes including water depth, wave action, oxygenation, food supply, substrate type, turbidity, and insolation. The distribution of molluscs along this radial environmental gradient has been plotted as the distance of collecting sites from the nearest presumed atoll edge at the time of deposition (i.e. the edge of the present seaward platform).



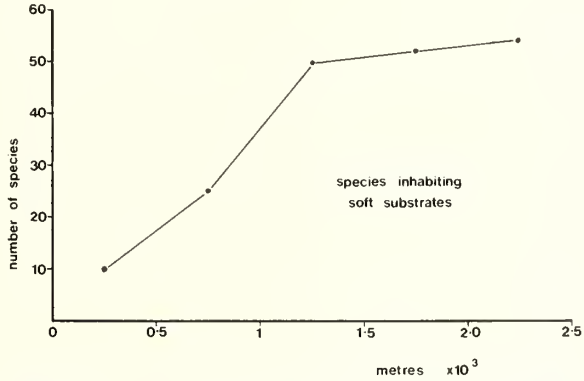
TEXT-FIG. 6. Molluscan species richness plotted against radial distance from the atoll edge. Collecting sites were grouped into 500-m increments and the average number of species plotted against the mid-point of the distance group.

Total molluscan species richness (text-fig. 6) shows a maximum at about 1000 m from the atoll edge with a rapid decline towards the atoll edge and a more gradual decrease towards the centre. However, text-fig. 7 shows that there are appreciable differences from one end of the atoll to another; thus along an east-west line there are about twice as many species at the western than the eastern end.



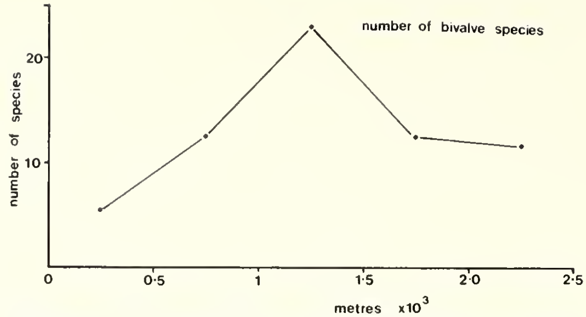
TEXT-FIG. 7. Molluscan species richness plotted against the distance along the west–east axis of the atoll during Aldabra Limestone times.

Text-fig. 8 shows the percentage of numbers of species which normally live on soft substrates; there is a rapid increase from 10 to 50% up to about 1200 m from the edge, the numbers thereafter remaining fairly constant towards the centre of the atoll. In common with the total species richness the greatest number of bivalve species (text-fig. 9) is found 1250 m from the atoll edge, whereas over most of the rest of the distance numbers remain at less than 15% of the total fauna. However, the numerical proportion of bivalve individuals in samples (text-fig. 10) increases from about 25–50% in the distance from the outside to the inside of the atoll.

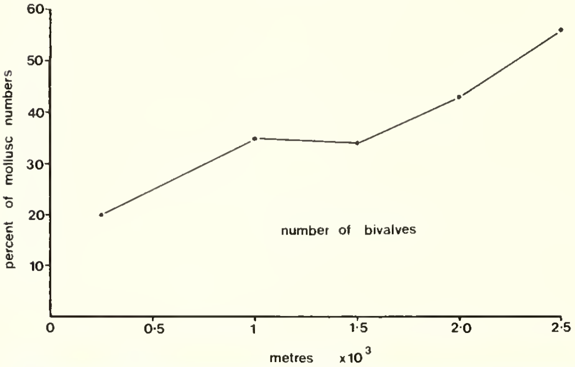


TEXT-FIG. 8. Number of mollusc species normally inhabiting soft substrates plotted against radial distance from the atoll edge during Aldabra Limestone times.

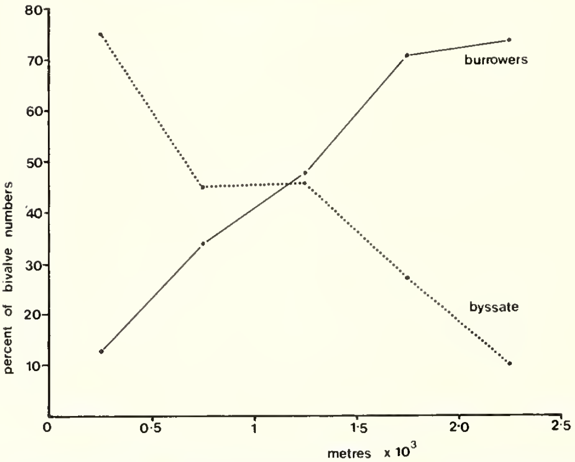
If the bivalve component of the samples is broken down into life-habit categories, then the two most important divisions into byssate and burrowing species show interesting distributions (text-fig. 11). Byssate species comprise about 75% of bivalve individuals at the outer edge of the atoll but decrease rapidly towards the interior. In contrast, burrowing species are poorly represented at the edge but rise to about 75% in the interior.



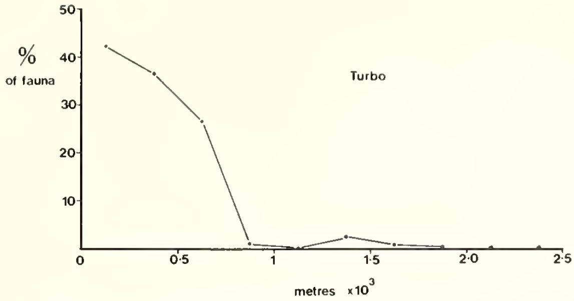
TEXT-FIG. 9. Number of bivalve species plotted against distance from the atoll edge during Aldabra Limestone times.



TEXT-FIG. 10. Percentage of molluscan numbers comprised by bivalves plotted against distance from the atoll edge during Aldabra Limestone times.

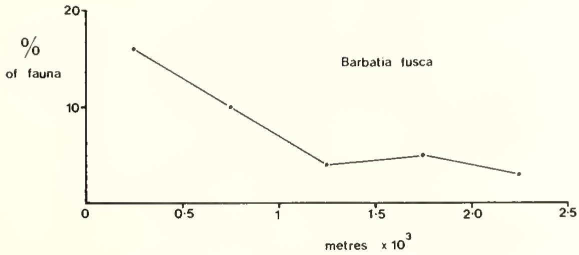


TEXT-FIG. 11. Percentage of bivalve numbers represented by two life habitat categories of byssally attached and burrowing, plotted against radial distance from the atoll edge during Aldabra Limestone times.



TEXT-FIG. 12. Percentage of *Turbo* individuals in total mollusc fauna plotted against distance from the atoll edge during Aldabra Limestone times.

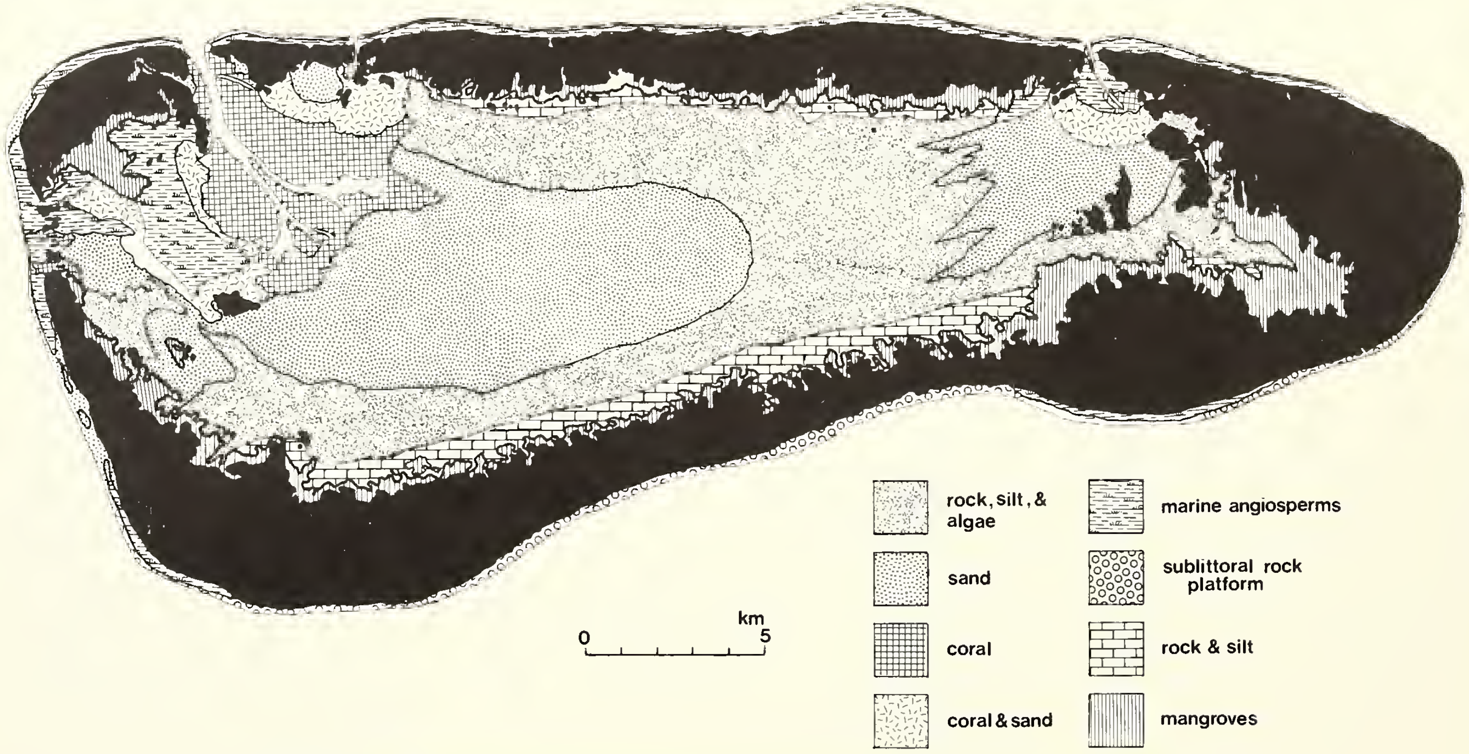
The distribution of individual taxa show similar trends. Thus *Turbo* remains a major component of samples at the atoll edge (text-fig. 12) and comprises an average of about 40% of the total fauna, but is virtually absent by about 900 m from the edge. A similar, but more gradual decrease in importance inwards is shown by the byssate *Barbatia fusca* (text-fig. 13).



TEXT-FIG. 13. Percentage of *Barbatia fusca* individuals in total mollusc fauna plotted against distance from the atoll edge during Aldabra Limestone times.

Although there are no studies of molluscan faunas from complete analogues of the Aldabra Limestone environment, there are descriptions of faunas from individual habitats which are comparable. For instance *T. argyrostomus*, *Trochus* species, and abundant *B. fusca* have been recorded from *Acropora*-dominated reef edges and patch reefs around Mahé, Seychelles (Taylor 1968). *Turbo* and *Trochus* species are among the dominant molluscs on seaward, wave-exposed reef edges of many Indo-Pacific atolls (Morrison 1954; Demond 1957; Salvat 1970; Taylor 1971*a*; Kay 1971).

The families Strombidae, Cerithidae, Naticidae, Tellinidae, and Veneridae are the dominant taxa in many shallow atoll lagoons (Salvat 1967, 1972; Kay and Switzer 1974; Morrison 1954). The habitats and fauna described by Wells (1957) for leeward lagoon reefs with patch reefs of *Porites* separated by sandy areas and abundant *Halimeda*, seem to be very similar to the environments present within the atoll rim during Aldabra Limestone times.



TEXT-FIG. 14. Generalized map of the major shallow-water habitats of Aldabra at the present day.

PRESENT-DAY HABITATS AND FAUNA

In the context of the geological sequence on Aldabra the present day can be considered as an erosional event. It is thought that sea-level has been at approximately the same position since about 3000–5000 years ago, and thus present-day habitats and communities have developed since this time.

Details of the geomorphology have been given by Stoddart *et al.* (1971) and Braithwaite *et al.* (1973) and only the major features are outlined below. A nearly continuous elevated land rim breached at four places by narrow channels surrounds a shallow lagoon. On the seaward side the land is terminated by steep cliffs 4 m high beyond which is an intertidal and shallow subtidal platform up to 400 m wide which ends abruptly at the steep seaward slope of the atoll. The lagoon is almost completely fringed by mangroves which are growing upon rock or silt substrates (Macnae 1971). The rest of the lagoon floor, which rarely exceeds 5 m in depth, is generally rock bottomed but may have a thin cover of fine sand or silt. Near the channels the hydrodynamic situation is much more complex and a mosaic of habitats is developed, with accumulations of sand, beds of marine angiosperms, coral patches, and mixed sand and coral areas (text-fig. 14). Details of the seaward slope of the atoll have been described by Taylor (1971*b*). Along the southerly and easterly coasts the seaward platform consists of algal-covered rock pavement, but at the northerly and westerly ends of the atoll the rather wider platform is covered by beds of marine angiosperms and some mobile sand bodies. Along the seaward edge of the platforms there is usually a zone consisting of loose limestone blocks (the boulder zone) resting upon rock substrate. The seaward slope of the atoll is mainly rocky, with extensive coral growth only at the western end (Barnes *et al.* 1971). More detailed description of the Recent molluscan fauna will be published elsewhere but some idea of the composition and relative abundance of molluscs from some of the major habitats is given below (text-figs. 15, 16) so that comparison may be made with the fossil assemblages.

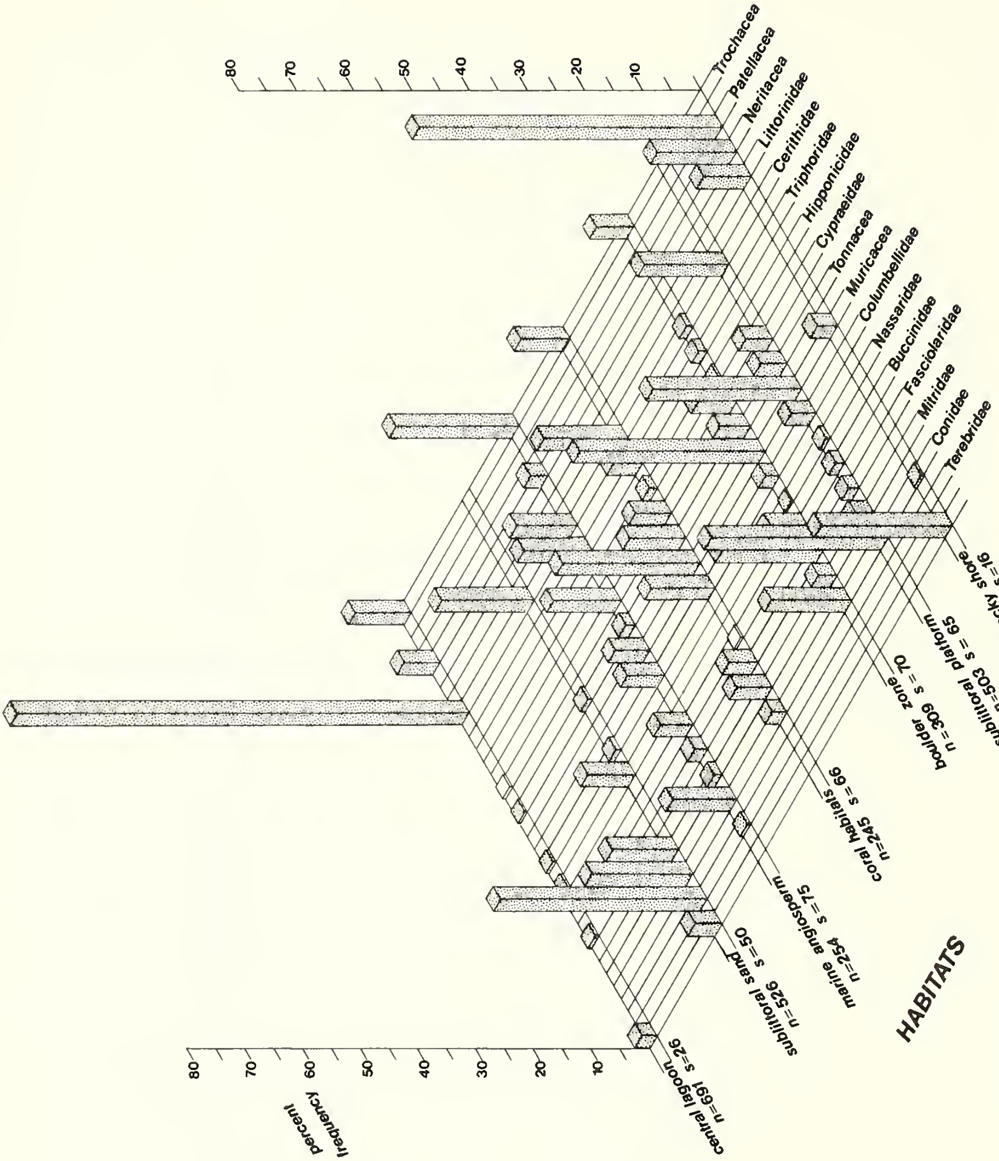
Intertidal rocky shores

The faunas from this habitat have been described by Taylor (1971*b*, 1976) and Hughes (1971). The dominant gastropods are the prosobranch limpets *Acmaea* and *Cellana* and the pulmonate limpet *Siphonaria*. Other algal grazers include five species of *Nerita* and four of *Littorina*. The main predators present are the muricid gastropods *Thais*, *Purpura*, and *Morula*. The cemented vermetid gastropods *Dendropoma* are extremely abundant on the lower shore but have not been included in these counts.

The most abundant bivalves on more sheltered rocky shores are the Mytilacea with *Brachiodontes variabilis* occurring in dense patches in the low intertidal zone and *Lithophaga* boring into the limestone. The pteriacean *Isognomon dentifer* is common byssate in high crevices and the oyster *Saccostrea cuccullata* is common at mid-shore at some sites.

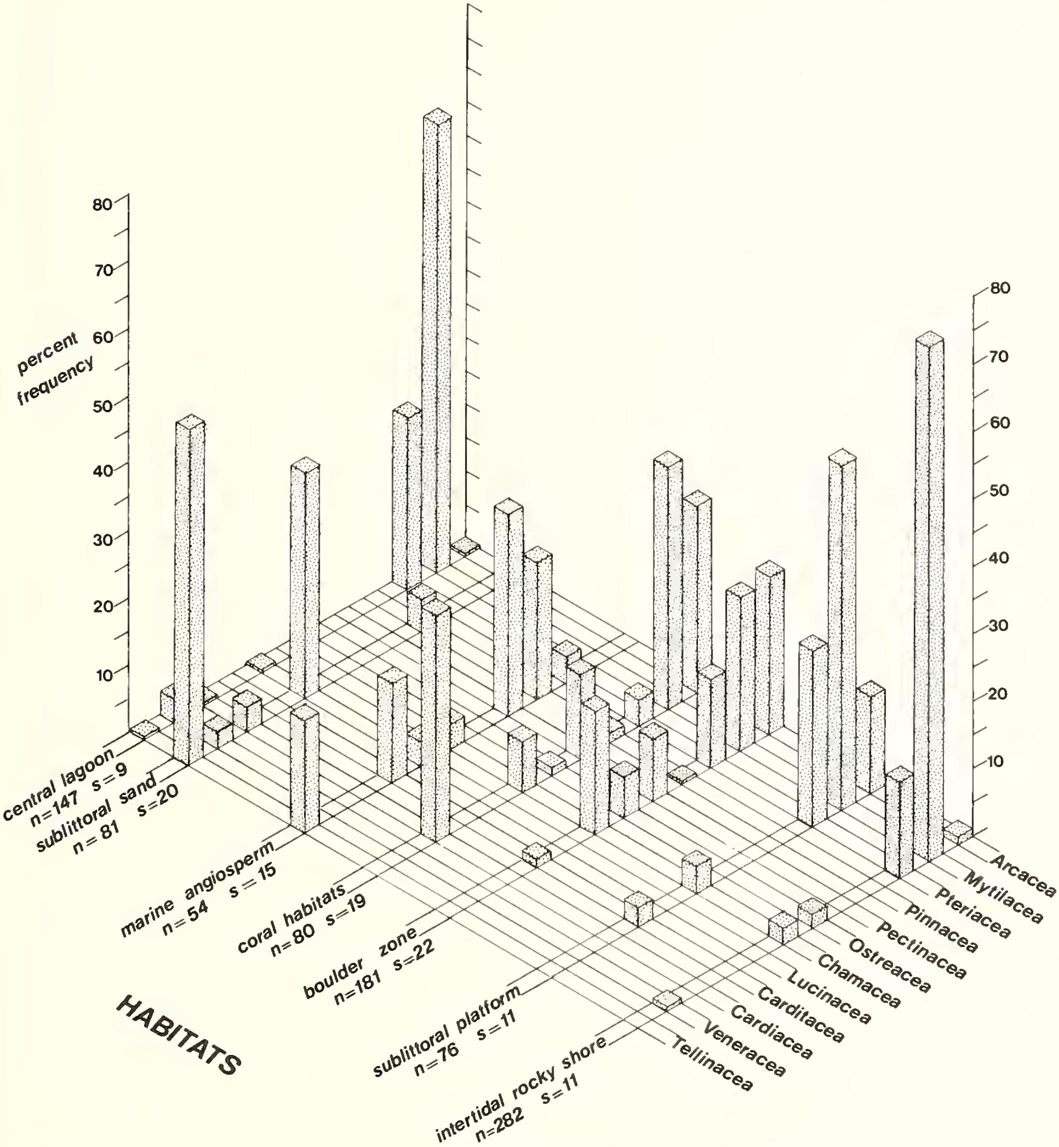
Sublittoral rock platforms

This habitat is developed mainly around the southern and eastern shores of the atoll. Amongst the gastropods the Muricacea (26%) and the Conidae (31%) are the dominant



TEXT-FIG. 15. Relative abundance of families and superfamilies of gastropods in some of the major shallow-water habitats of present-day Aldabra. Data from quantitative samples. n = number of individuals; s = number of species.

taxa, the most abundant forms being species of *Morula*, *Drupa*, and many species of *Conus*, particularly *C. ebraeus*, *C. rattus*, and *C. flavidus*. Other predators are *Engina* and *Peristernia* of the Buccinidae and Fasciolaridae and several species of *Strigatella* (Mitridae). The Cerithidae (9%) comprise mainly small species found in the algal turf. *Cypraea caputserpentis* and *C. histrio* are the most common Cypraeidae and the Tonnacea are represented by *Bursa granularis* (6%).



TEXT-FIG. 16. Relative abundance of bivalve superfamilies in some of the major habitats of present-day Aldabra. Data from quantitative samples. n = number of species; s = number of individuals.

Bivalves are not abundant and are represented by only eleven species. Mytilacea again dominate the fauna with *Modiolus auriculatus* the most common. The Pteriacea with *Isognomon perna*, *I. legumen*, and *Pinctada* are byssate in crevices. Another byssally attached crevice form, *Barbatia helblingi* (Arcacea 15%), is the only other common bivalve.

Platform edge and boulder zone

The gastropod fauna is dominated by Muricacea (41%), mainly by species of *Drupa*, *Morula*, *Mancinella*, and *Maculotriton*. The Fasciolaridae (18%) are abundant, and *Peristernia* and *Leucozonia* are the common forms. Many species of *Conus* are present (Conidae 14%) as well as some small species of Turridae. Other families, the Trochacea, Cypraeacea, and Tonnacea, are all present at about 5%.

This habitat supports quite a diverse fauna of byssate and cemented bivalves and species of Arcacea (23%) include *B. helblingi*, *B. tenella*, and *Arcopsis symmetrica* common beneath blocks and in crevices. The Mytilacea (23%) include byssate forms such as *Modiolus*, *Brachiodontes*, and *Septifer*, but also boring *Lithophaga* species. Small *Pinctada* and *Isognomon* (Pteriacea 13%) are common beneath the blocks as is *Chlamys cuneolus* (Pectinacea 9%).

Coral-dominated habitats

The most prolific coral growth areas occur in the lagoon channels and on the front of the seaward platform at the western end of the atoll. The coral areas differ considerably in species composition and complexity, but all samples have been combined in text-figs. 15, 16.

The gastropod fauna from coral habitats is quite diverse, but the Muricidae are the dominant taxa comprising 15% of the fauna with *Morula uva* and the coral-feeding *Drupella cornus* the most common species. Other important taxa are *Columbella turturina* (Columbellidae 11%), the Coralliophilidae (9%) with *Quoyula* and *Coralliophila*, the Fasciolaridae with *Latirus* and *Peristernia*, and the Mitridae (6%). Many small gastropods occur in these habitats, particularly species of *Rissoina* (Rissoidae 11%), Triphoridae (5%), and Cerithidae (4%).

Bivalves are not abundant, although the habitat supports quite a diversity of byssate and cemented forms with members of the Arcacea, particularly *Barbatia helblingi*, the most abundant. *Cardita variegata*, another byssate species, is also very abundant. The Mytilacea are mainly represented by several species of borers *Lithophaga* and *Botula*.

Marine angiosperm habitats

These are present on the northern and western seaward platforms and in the lagoon near the channels. The most dominant gastropods are the Trochacea (22%) with *Phasianella aethiopica*, *Turbo spinosus*, and *Infundibulum erythraeus* the most common species. The small neritacean *Smaragdia* is common on the leaves of the grasses. Other common families are the Triphoridae (12%), the Cerithidae, mainly *Cerithium rostratum* and *Rhinoclavis asper*. The Cypraeidae comprise 12% of the sample, and mainly inhabit the undersides of dead coral blocks and cobbles, although a few species are found living upon the marine angiosperms. *Strombus gibberulus*, *S. muta-*

bilis, and *Lambis truncata* are often common on the substrate surface, whilst species of *Morula* are found on the blocks and cobbles.

Surprisingly the bivalve fauna is rather sparse, with the most common form, *Chlamys cuneolus* (Pectinacea 35%) being found byssate beneath cobbles. Infaunal suspension feeders *Pinna muricata* and *Atrina vexillum* are locally common. The Tellinacea (16%) are the most abundant burrowing group, and a few Lucinacea occur.

Sublittoral sand habitats

Most of the sublittoral sand habitats are located in the lagoon near the lagoon channels. Amongst the gastropods the numerically dominant taxon is the predatory family Terebridae, represented by twenty-two species and comprising 36% of individuals. Two species of *Conus*, *C. arenatus* and *C. tessulatus*, are also important (Conidae 18%). Other important predatory groups living in the sand are the Mitridae (7%), Vexillidae (5%), and the scavenging Nassaridae (8%). The only other numerically important group is the Cerithidae (16%) mainly represented by *Rhinoclavis asper* and *Cerithium echinatum*.

This habitat supports quite a diverse bivalve fauna dominated by burrowers, particularly the Tellinacea (49%), including species such as *Tellinella crucigera*, *T. staurella*, *Jactellina clathrata*, and *Scissulina dispar*. The other most common group is the Lucinacea, with *Codakia punctata*, *Anodontia edentula*, and *Diplodonta* the more abundant species.

Central lagoon habitats

The turbid central lagoon is the greatest area of shallow-water habitat available at Aldabra and is occupied by an essentially uniform fauna. The fairly shallow more or less silt-covered rock substrate is covered with the algae *Halimeda*, *Hydroclathrus*, *Cystosiera* and *Caulerpa*, and sponges.

The Mollusca inhabiting this habitat are dominated by Cerithiacea, and in particular by two species, *Cerithium morum* and *C. rostratum*, which occur in great abundance. Few other macrogastropod species occur, and these include *Infundibulum erythraeus*, *Peristernia*, and occasional *Cypraea* and *Pyramidella*.

The most common bivalve in the lagoon is the small byssate *Brachiodontes variabilis* attached to rock surfaces, and *Vulsella vulsella* is common commensal among the benthic sponges. Infaunal bivalves are uncommon except near channels where sediment is thicker and *Scissulina dispar* and *Jactellina* may occur.

Mangrove habitats

Mangrove habitats are developed around the margins of the lagoon, and the faunas inhabiting them vary according to the substrate type. At the outer edges the mangrove faunas merge transitionally into lagoon faunas. Cerithiacea are the dominant gastropod super family with *Terebralia palustris* and *Cerithium morum* occurring in immense numbers on the substrate beneath the mangroves. *Littorina scabra* is common on the trunks and leaves of the mangroves and *Nerita undata*, *Siphonaria*, and the large chiton *Acanthopleura* are common on rock outcrops within the mangrove habitats. Bivalves are not common, although *Isognomon dentifer* and *Brachiodontes* may be found on the rocks and *Quidnipagus palatum* in the silt.

CONCLUSIONS

The three successive molluscan faunas described from the Pleistocene rocks of Aldabra Atoll, coupled with the present-day fauna, give some insight into the evolution of the present-day marine faunas of Aldabra. Each of the faunas is very different in character and this is a reflection of the changes in habitat structure of the shallow-water marine environment accompanying each geological event.

The Esprit Limestone fauna, dominated by infaunal bivalves and cerithiid gastropods, lived in sublittoral to intertidal sandy, probably lagoonal, conditions. It must be stressed that the rocks exposed represent only a small fraction of the atoll area at this time.

The Takamaka Limestone fauna, dominated by trochacean gastropods, inhabited a wide shallow bank with abundant crustose coralline algae, corals, possibly the marine angiosperm *Thalassodendron*, and with calcareous muds in quiet water areas. Conditions were apparently fairly uniform over the whole atoll. The Aldabra Limestone fauna inhabited a shallow bank with abundant coral growth around the rim passing inwards into more sandy areas with abundant *Halimeda* and coral patches and knolls. The molluscan fauna was highly diverse and an abundance of *Turbo* and trochacean gastropods, epifaunal byssate, and cemented bivalves inhabited the atoll rim, with many Cerithidae, Strombidae, and burrowing bivalves in the more sandy areas within.

At the present day the large, shallow, turbid lagoon supports abundant cerithiid gastropods, but the more varied coralline, marine angiosperm, and sandy habitats around the channels support a much more diverse fauna. The seaward sides of the atoll are surrounded by limestone cliffs and the more exposed parts of the seaward platform covered by an algal turf with stands of marine angiosperms in the more sheltered parts. Epifaunal gastropods and byssate and cemented bivalves dominate in these seaward habitats.

Similar large-scale changes in the habitat structure of reefs are seen elsewhere; for instance, recent studies of the Pleistocene limestones of the Kenya coast (Crame 1976) have shown that during the last interglacial Kenya was probably bordered by linear patch reefs with a broad back reef area consisting of sands with abundant *Halimeda* and coral knolls. Today, by contrast, the present 'reef' is a broad, shallow, erosional platform cut into elevated Pleistocene limestones. Present-day coral growth is limited in extent and very localized. Assemblages of molluscs very different from those occurring today have been obtained from the Pleistocene limestones. Similarly, Kay and Switzer (1974) report fossil Mollusca in Fanning Island lagoon very different from those living there today.

Although there have been other taxonomic studies of Pleistocene Mollusca from other reef areas in the Indian Ocean (Cox 1927, 1930; Nardini 1934, 1937; Abrard 1942), comparison with the Aldabra sequence has been prevented by the lack of a reliable dating framework. It is apparent, however, that in these areas there has been considerable faunal change. The widely recognized 125 000-year-old limestone, representing sea-level from 2 to 10 m above the present, would make a suitable datum for the comparison of late Pleistocene reef faunas.

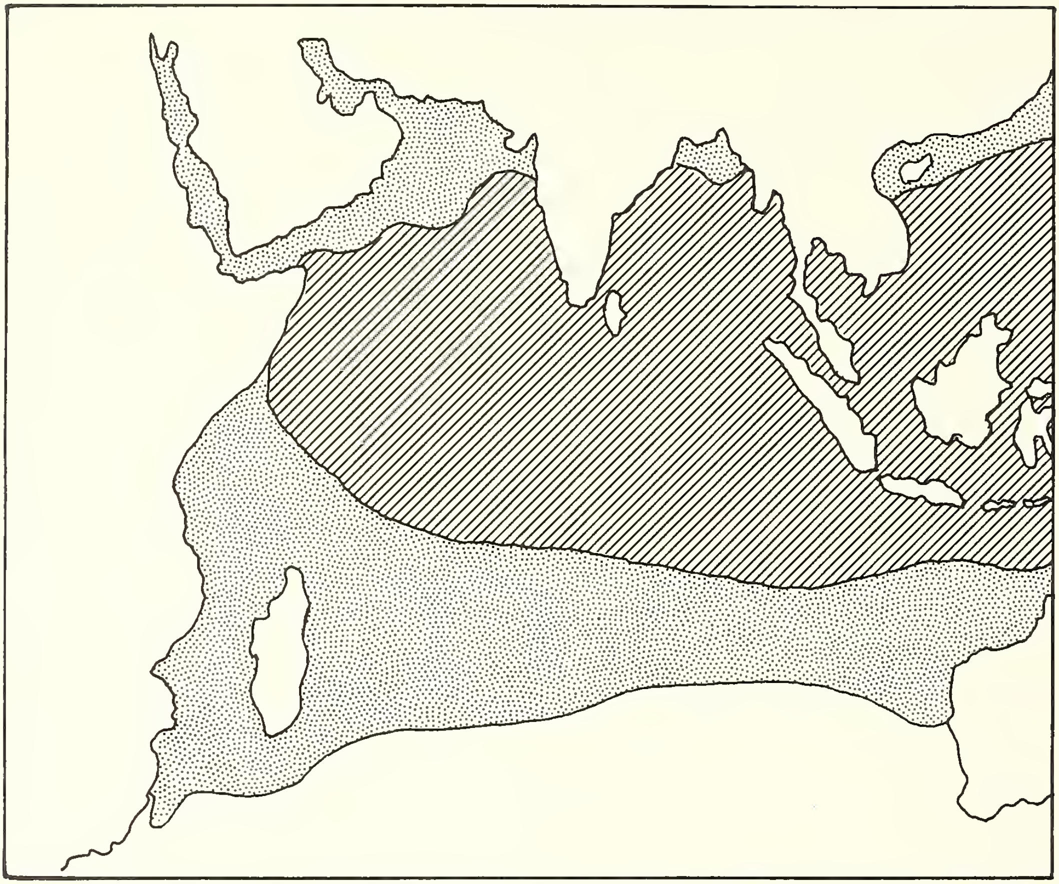
During the times of the late Pleistocene sea-level changes which have affected

Aldabra, there has obviously been a continuity of molluscan occupation of marine habitats but the faunas from the different stages that are preserved are very different in character. The three fossil faunas described all occur in beds representing depositional events associated with rising, and higher than present, sea-levels. Unfortunately there is no information about faunas which lived during times of erosional events when sea-level was falling or lower than present, or of depositional events from sea-levels significantly lower than present, which may have occurred in the last 125 000 years (Bloom *et al.* 1974). Evidence from the surface geology suggests that periods of erosion may have been of much longer duration than the depositional phases; Mesolella *et al.* (1970) suggests that only during about 35% of the last 600 000 years has there been active reef growth at Barbados. The present-day state of Aldabra can be considered as an erosional event, marked by lowering of the land surface, cliff retreat, and enlargement of the lagoon. Sediment deposition and coral growth is very limited and most of the deposits are probably ephemeral in nature. During times of lowered sea-level, for instance during the last glaciation, Aldabra stood as a steep-sided, rocky island, perhaps 130 m high. The surrounding sea was probably too cold to support active reef growth (text-fig. 17) and sediment accumulation would have been minimal. The molluscan fauna inhabiting the limited shallow-water habitats of this rocky island would have been dominated by epifaunal and endolithic animals, and probably fairly similar in character to that fauna inhabiting the sublittoral and intertidal hard substrate habitats today. That is, an abundance of Patellacea, Neritacea, and Muricidae in the intertidal, and Trochacea, Cypraeidae, Muricacea, Buccinidae, and Conidae in the sublittoral zones.

It might be predicted that a progressive increase in sea-level will deepen and enlarge the present lagoon, resulting in improved circulation and sedimentation and encouraging a greater diversity of lagoon habitats. The seaward platform will be deeper and coral growth will probably increase. As a result of a relative rise in sea-level, molluscan diversity should thus increase as a result of the increased habitat diversity and the greater area available for colonization. As a result of increased and more stable sedimentation, the numbers of soft substrate-associated and burrowing species should also rise. By contrast, a lowering of sea-level will cause the emersion of the lagoon and seaward platforms, thus diminishing habitat space and faunal diversity. The fauna resulting from these changes will be predominantly epifaunal in character.

As well as the dramatic changes which affected the shallow-water benthos around Aldabra itself there were broad-scale habitat changes in other shallow-water areas of the western Indian Ocean that may well have affected the distribution of organisms. Thus, at the time of the maximum depression of sea-level during the last glaciation, most of the coral islands, atolls, and shallow banks of the area would have been emergent. The slopes of all these submarine features are steep and rocky, and the over-all area of soft substrates would have been considerably reduced, which should have affected the diversity of infaunal animals present in the area. Conversely the habitats available for rocky-shore and hard-substrate species were considerably increased, and diversity may have been higher.

It is apparent that relatively small changes in sea-level will cause large habitat changes on reefs, resulting in the destruction or formation of new habitats and causing either extinctions or opportunities for new colonizations. This might be exemplified



TEXT-FIG. 17. Possible extent of the contraction of the coral reef seas (i.e. within the 20° C. isotherm) of the Indian Ocean during times of glacial advance. Redrawn from Stoddart (1973), original data from palaeotemperature analyses. Cross hatching = water warmer than 20° C. during last glacial advance; stippling = water warmer than 20° C. at present day.

by the present shallow lagoon at Aldabra; a major event during the post glacial sea-level rise was the breaching of the land rim to form the present lagoon, an event which at once enormously increased the area of shallow-water habitat available for colonization by marine faunas. Because of the drastic effects resulting from small sea-level changes there has probably been more continuity of habitats and communities on continental margins and high islands than on atolls and low oceanic islands. The higher environmental and topographic complexity on continental margins must improve the chances of particular habitats surviving through rapid sea-level changes; whereas comparable changes on atolls would result in the complete elimination of habitats.

Most differences in the composition of successive faunas at Aldabra are obviously related to the different habitats available for colonization. However, as Diamond (1975) has discussed, the final species composition of the community may partly be determined by random factors such as the order in which colonists arrive, which may affect the admission of later arrivals into the community. Thus alternate stable communities can be assembled. The great variation seen in closed lagoon faunas of Pacific atolls may result from such random factors (Salvat 1967, 1972; Kay and Switzer 1974). However, the similarity of seaward reef faunas at various localities around the Indian Ocean suggests that upon seaward reefs such factors are unimportant (Taylor 1977).

It is also probable that during the late Pleistocene there have been changes in the tropical Indian Ocean species pool from which the Aldabra marine fauna has been recruited. Although our knowledge is incomplete, we are aware that the present-day species pool is not uniform; for instance, some species are restricted to continental margins and large islands whilst others are found only in parts of the region. Unfortunately few Pleistocene faunas have been investigated in sufficient detail for comparisons to be made. However, that such changes have occurred is evidenced by the bivalve family Tridacnidae which are taxonomically and zoogeographically well known (Rosewater 1965). At Aldabra, five species are found in Pleistocene rocks, *Tridacna maxima*, *T. squamosa*, *T. crocea*, *T. gigas*, and *Hippopus hippopus*, whilst only two, *T. maxima* and *T. squamosa*, are found at the present day. *Hippopus* occurs in the Esprit and Takamaka Limestones, *T. gigas* and *T. maxima* in both the Takamaka and Aldabra Limestones and *T. crocea* and *T. squamosa* in the Aldabra Limestone. *Hippopus*, *T. gigas*, and *T. crocea* are at the present day restricted in distribution to the Indonesian–W. Pacific area, and are absent from the Indian Ocean west of Sumatra. *T. gigas* and *T. crocea* have been similarly recorded from Pleistocene rocks of the Kenya coast (Crame 1976). There have thus been major changes in the distribution of *Tridacna* species since the last interglacial period 125 000 years ago. Similar changes are known in other groups, for instance the mangrove-associated gastropod *Cerithidea*, now restricted to continental margins in the Indian Ocean, was present in the Esprit Limestone of Aldabra.

Implicit in many hypotheses concerning the high diversity of tropical areas compared with high latitudes is the idea of the stability of the tropical environment over long periods of both ecological and evolutionary time (Pianka 1966; Pielou 1975; Sanders 1968, 1969). Along with tropical rain forests, coral reefs are usually cited as the most diverse and complex ecosystems to have evolved.

We know from the studies at Aldabra and from many other reef systems in the Indo-Pacific area that during the late Pleistocene, reef systems have certainly not been stable, and periods of active reef growth have alternated with emergence and erosion (Tracey and Ladd 1974; Purdy 1974; Brousse *et al.* 1974; Stoddart 1976). Moreover, many reefs on tectonically active shores have been either elevated high above sea-level or submerged too deeply for coral growth to proceed (Bloom *et al.* 1974; Chappell 1974*a*; Mesolella *et al.* 1970). Following the high sea-level stand of the last interglacial about 125 000 years ago there was a progressive but oscillating decrease in sea-level to about 17 000 years ago, at the height of the last glaciation when sea-level stood about 130 m below the present (Chappell 1974*b*). This would have exposed all the present shallow-water habitats of coral islands and atolls of the Indian Ocean high above sea-level. The subsequent and rapid (*c.* 1 m/100 yrs) post-glacial rise in sea-level reached approximately the present position about 5000 years ago. It follows, therefore, that most reef habitats and the communities inhabiting them have developed during this time. Thus in talking about the evolution and survival of reef faunas we are referring to the stability of the faunal province and species pool in general, and not to the stability of individual reef systems which are clearly unstable over evolutionary time.

The Indo-West Pacific marine province forms a more or less stable species pool from which the faunas of individual reef systems are recruited. The uniform thermal conditions over much of the area, the broad latitudinal extent, and the great variation in tectonic style and hence habitat diversity, has ensured the long-term continuity of the faunal province. The dimensions of the whole province, however, must have changed considerably during the cooling and warming periods of glacial advance and retreat. Reference to text-fig. 17 shows that the area occupied by the tropical species pool in the Indian Ocean was probably reduced by about 50% during the last glacial maximum. The highest diversities of the Indo-Pacific province are found in the Indonesian area (Stehli 1968; Valentine 1971, 1973) which is also the tectonically, and hence environmentally, most complex; an extensive subduction zone is marked by east-west chains of trenches, mountains, and island arcs bordering the continental margins of Asia and Australia. The Indo-Pacific species pool has thus been able to survive the climatic disturbance of the glacial advances which resulted in provincial retraction and widespread habitat changes. With some exceptions, species have been able to recolonize into areas from which they were probably excluded during periods of global cooling, even though reef habitats have drastically changed.

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JURASSIC-CRETACEOUS BIOSTRATIGRAPHY OF NORWAY, WITH COMMENTS ON THE BRITISH *RASENIA CYMODOCE* ZONE

by T. BIRKELUND, B. THUSU, *and* J. VIGRAN

ABSTRACT. Extensive collections from exposed and mechanically excavated sections permit the recognition of Middle Jurassic to Neocomian deposits in Andøya, northern Norway. Non-marine Bajocian-Bathonian is recognized by an assemblage of spores and pollen showing a close resemblance to that from the Middle Jurassic of Trøndelag, Scania, and the Netherlands, but with some differences from Middle Jurassic assemblages from Britain. Marine Upper Jurassic sediments contain ammonites and dinocysts that permit the recognition of the *Rasenia cymodoce* Zone of the Lower Kimmeridgian, and the *Pavlovia rotunda–Progalbanites albani* zones of the Middle Volgian. The Upper Ryazanian *Surites spasskensis* Zone is the only zone recognized in the Neocomian sequence, but dinocysts, buchias, and ammonites suggest the presence of Valanginian beds above the *S. spasskensis* Zone. The boreal fauna shows close affinities with faunas from England, East Greenland, and Siberia. Similarly, dinocyst assemblages are comparable with those from other areas in north-west Europe and the Arctic, but the Ryazanian–Valanginian dinocyst assemblage shows closer links with boreal assemblages from Spitsbergen, the Moscow Basin, and the North Slope of Alaska. On the basis of material from Market Rasen (England) and Andøya the subdivision of the *R. cymodoce* Zone is discussed.

OUTCROPS of *in situ* Mesozoic rocks in Norway are known only from the island of Andøya, located just north of the Lofoten Islands (text-fig. 1). The great distances that isolate Andøya from other exposures of the same age render the island a vital link in palaeogeographic reconstruction. There are in addition Jurassic erratics in the Trøndelag area (text-fig. 1).

Andøya

The Jurassic and Lower Cretaceous rocks of Andøya occupy an area of approximately 8 km^2. The sequence is some 650 m thick (text-fig. 2) and consists predominantly of sandstone and shale resting unconformably on weathered Precambrian basement. Except to the south, the outcrop area is bounded by faults. The sediments thicken to the east and appear to extend offshore into Andfjord. The 5 km of sediments shown to occur in the outer part of the fjord by seismic evidence (Sundvor and Sellevoll 1969) may, in part, be a continuation of the Andøya sequence.

The tight pattern of post-Lower Cretaceous faults has created two small troughs, one in the north and one in the south. The southern trough contains rocks of mainly Middle and late Jurassic age, whereas Lower Cretaceous rocks make up the bulk of the sequence in the northern trough. Both troughs are connected by a thin sedimentary cover across a basement high.

Previous lithostratigraphic and palaeontological work has been carried out mainly by Vogt (1905), Sokolov (1912), and Ørvig (1953, 1960), and a number of other early works containing important stratigraphic information are listed in text-fig. 2. Recently Dalland (1975) established a new stratigraphic nomenclature on the basis of surface and mechanically excavated sections (text-fig. 2). The present paper is

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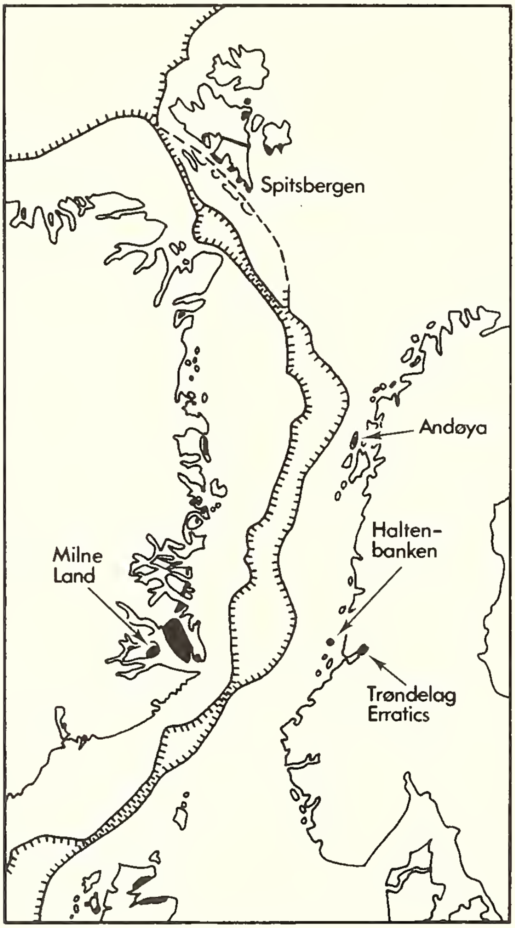
based on samples collected by Dalland during extensive sedimentological and stratigraphic studies.

The Jurassic rocks include the Ramså Formation and the main part of the Dragneset Formation (text-fig. 2). The Ramså Formation consists of sandstone, shale, siltstone, and coal layers. The lower part of the overlying Dragneset Formation consists of medium- to fine-grained sandstone, and the middle part is a monotonous sequence of siltstone and fine-grained sandstone, while the upper beds are predominantly shale.



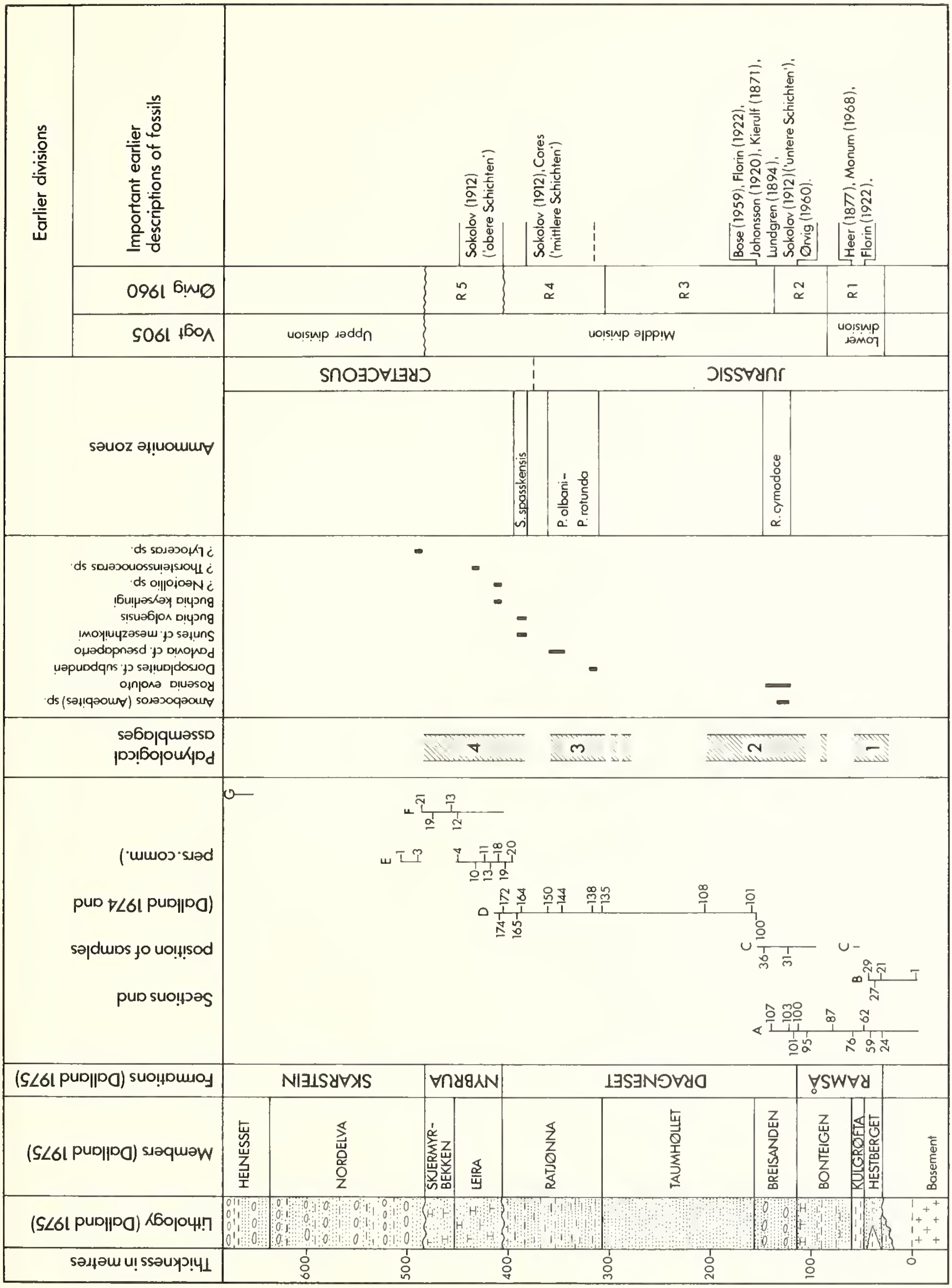
TEXT-FIG. 1. Map of the northern Atlantic area prior to the opening of the Ocean. Jurassic outcrops of Norway, Spitsbergen, East Greenland, and northern Scotland indicated. Ticked lines denote margins of continental blocks. Palinspastic reconstruction after Birkenmajer (1975).

The Cretaceous rocks include the uppermost part of the Dragneset Formation, and the Nybrua and Skarstein formations (text-fig. 2). The Nybrua Formation consists of calcareous sandstone and siltstone, and according to Dalland (1975) the boundary with the Dragneset Formation appears to be an unconformity. The Skarstein Formation, which probably lies unconformably on the Nybrua Formation, comprises siltstone and silty shale in the lower part, and mudstone, shale, and thin beds of sandstones in the upper part. The sandstone layers show graded bedding and other structures commonly found in turbidites.

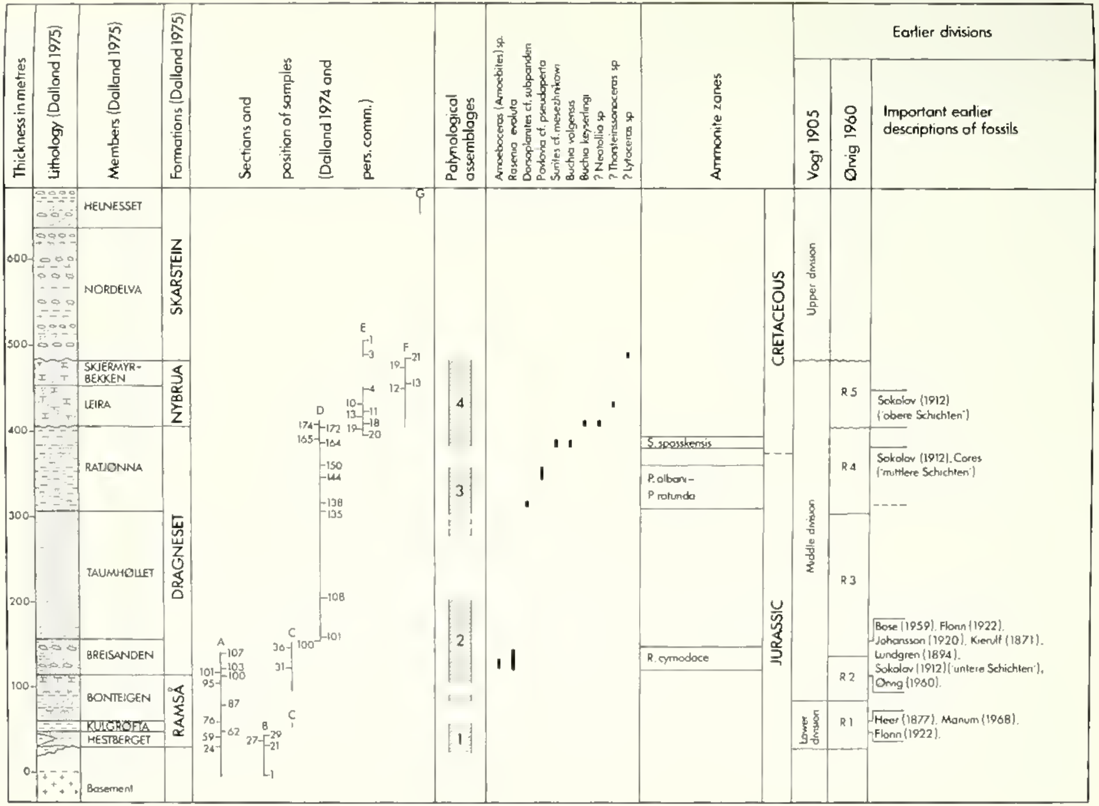
Dalland (1975) considered the lower, coal-bearing part of the sequence to be a fresh- to brackish-water deposit, while most of the overlying Jurassic sequence was referred to littoral environments, shallow, brackish-water lagoons, or mud flat deposits. However, no lithological evidence of littoral or lagoonal environments was given, and the fossil content indicates a sublittoral origin for considerable parts of the sequence. The Cretaceous sequence was considered by Dalland to be marine, the early part being deposited in shallow, sublittoral environments, and the later part in deeper water.

Trøndelag

Locally derived glacial erratics composed of sideritic ironstone and calcareous sandstone of Middle Jurassic age are found in the Trøndelag area (text-fig. 1). In a detailed study Oftedahl (1972) found sideritic ironstone boulders confined mainly to the stony beaches along the inner western shores of Trondheimsfjord. Plant



TEXT-FIG. 2. Jurassic and Lower Cretaceous succession of Andøya.



TEXT-FIG. 2. Jurassic and Lower Cretaceous succession of Andøya.

cuticles described from this material (Vigran 1970) closely resemble those present in the Middle Jurassic of Yorkshire. Oftedahl (1972) considered the sideritic ironstone to be a lacustrine deposit, and that the erratics were derived from a Mesozoic, down-faulted basin in Beitstadfjord, in the inner part of Trondheimsfjord.

Grabs and core samples consisting of sandstones and soft clays recovered from Haltenbanken (Thusu and Vigran 1975) yielded palynomorphs of Middle Jurassic age, similar to those recovered from the erratics from Trøndelag.

Calcareous sandstone erratics have been recorded so far only from a group of islands, Froøyene, off the coast of Trøndelag (Oftedahl 1972). The fauna of these sandstones has been studied by J. Nagy (pers. comm.) who reports bivalves, gastropods, cephalopods, and anellids of Middle Jurassic age. This sandstone is thought to have been derived from a local sedimentary basin off the Trøndelag coast (Oftedahl 1975).

BIOSTRATIGRAPHY

The biostratigraphy presented below is based on ammonites and buchias as well as pollen, spores, and dinocysts. It is our hope that the combined use of macrofossils and microfossils will support the correlation of the Jurassic–Lower Cretaceous of the North Atlantic with classical standard zonations.

Ammonites and buchias

Earlier work on the fauna of the Jurassic–Cretaceous sequence of Andøya by, for example, Lundgren (1894), Sokolov (1912), and Ørvig (1953, 1960) shows the presence of Lower Kimmeridgian–Valanginian deposits, but the old collections are difficult to place exactly in relation to the new bed-by-bed collections reported in this paper. Only species of special stratigraphic importance from the old collections are therefore discussed here.

Text-fig. 2 shows the stratigraphic distribution of ammonites and buchias in relation to the lithostratigraphic divisions established by Dalland (1975).

Breisanden Member. The 40-m thick, sandy Breisanden Member contains *Rasenia evoluta* almost throughout its sequence, while *Amoeboceras* (*Amoebites*) sp. occurs in the lower beds. *R. evoluta* is closely allied to *R. uralensis* (d'Orbigny, 1845), and on this basis the Breisanden Member is referred to the *R. cymodoce* Zone of the Lower Kimmeridgian.

The *R. cymodoce* Zone was introduced by Salfeld in 1913 and 1914 (in the first attempt at a zonal classification of the Kimmeridgian in NW. Europe) and is bounded by the *Pictonia baylei* and *Aulacostephanus mutabilis* zones below and above respectively. Salfeld also cited *R. uralensis* as a diagnostic species, and it has since become clear that the beds of the *R. cymodoce* Zone yield a number of distinguishable faunas.

Spath (1935, p. 72) suggested that the two forms recognized by Salfeld, *R. cymodoce* and *R. uralensis*, are successive in time. *R. cymodoce*, still close to *Pictonia*, is the older. *R. uralensis* (here included in *R. evoluta*), typical of the sequence at Market Rasen (England), and never associated with *Prorasenia*, is the younger. A division of the *R. cymodoce* Zone into a restricted *R. cymodoce* Zone or Subzone below and a

R. uralensis Zone or Subzone above has been used more or less informally since 1935 by a number of authors. Besides the Market Rasen fauna from Lincolnshire, a Scottish fauna from Eathie, Ross-shire, has also been referred to the *R. uralensis* Zone by Waterston (1951) and Ziegler (1963). This fauna is, however, clearly distinguishable from the Market Rasen fauna. It is characterized by *R.* (*Semirasenia*) *askepta* Ziegler, 1963 (M) and *R.* (*Rasenioides*) spp. (m), all closely allied to *Aulacostephanus*.

Since Salfeld's accounts, no proper revision of the stratigraphy of this part of the succession has been published, and neither has a systematic description been made of the genus *Rasenia* since Spath's notes of 1935. The critical successions are those in Britain and the coast of Normandy, and a monographic treatment is badly needed. Some progress could be made by a brief examination of some of the more readily accessible English collections and exposures, although this is far beyond the scope of the present work. Good material is housed in the British Museum (Natural History), the Institute of Geological Sciences (London), and the Sedgwick Museum (Cambridge); and we have examined sections at the Blue Circle Portland Cement Group's clay-pit at Westbury, Wiltshire, and the foreshore of the Fleet south-west of Wyke Regis, Weymouth, Dorset (map of Arkell *et al.* 1947, fig. 2, p. 14). The Westbury section shows Kimmeridge Clay with abundant ammonites from the *R. cymodoce* to *A. eudoxus* zones, and has not yet been described. The Fleet section is badly slumped, and the beds must be exposed by digging. The dip is gently and steadily to the south so that the sequence of faunas follows simply from their position along the beach. The *R. cymodoce* Zone appears to be largely complete and in clays except for a prominent siltstone near the base, perhaps a metre thick, current-bedded, and packed in its lower part with bivalves (at least seventeen species), gastropods, and occasional ammonites. This bed was mentioned by Arkell (1947, p. 88) and may be called the Wyke Siltstone.

Taking the evidence together, it seems that the following four horizons with different *Rasenia* faunas can be distinguished in the *R. cymodoce* Zone. From below:

Horizon I. Rasenia cf. *cymodoce* (d'Orbigny, 1850) (M) and *R.* (*Prorasenia*) cf. *triplicata* (Sowerby) Spath, 1935 (m). Occurrence: Wyke Siltstone, the Fleet shore, Wyke Regis, Dorset.

Horizon II. R. (*Rasenia*) *involuta* Spath, 1935 (m) and *R.* (*Eurasenia*) spp. (M): Market Rasen fauna **A.** The famous fauna of splendidly preserved and iridescent shells, found in collections all over the world, is known only from museum material since the clays at Market Rasen are no longer exposed. A brief description of the former section was given by Woodward (1895, p. 175), who distinguished essentially 4–5 m of upper clays with small calcareous and pyritic concretions, resting on an unspecified thickness of lower, dark clays. Examination of the material in all three museum collections mentioned above, however, allows one to distinguish systematically two faunas differing in forms and preservation: fauna 1, consisting of involute adult and complete microconchs and nearly complete but always immature medium-sized macroconchs; and fauna 2, consisting of evolute mature and complete microconchs together with large, complete, and mature macroconchs. The shells of fauna 1 have the characteristic violet iridescence of the nacreous layer and lack the prismatic outer layer; the gas chambers of the phragmacone are still empty; and the body chambers are filled with a soft, buff, and probably somewhat phosphatic marly limestone. The shells of fauna 2 are only partly iridescent if at all, with a whitish layer, often encrusted with pyrite, and frequently embedded in septarian calcareous concretions. The differences in evoluteness were noted by Salfeld, who attached the MS names *involuta* and *evoluta* to specimens in the British Museum. Further descriptions are given below. Occurrence: (*a*) Market Rasen; (*b*) Wyke Regis, Fleet shore, in clays, with *R.* cf. and aff. *involuta* and *R.* (*Eurasenia*) sp., all crushed.

Horizon III. R. (*Zonovia*) *evoluta.* (M) and (m) (previously referred partly to *R.* (*Z.*) *uralensis* (d'Orbigny, 1845)): Market Rasen fauna **B.** Occurrence: (*a*) Market Rasen. The relative positions of faunas **A** and **B** have not been demonstrated at Market Rasen, but on morphological grounds there seems little doubt that **B** (*evoluta*) occurs above **A** (*involuta*); the *R. involuta* fauna still resembles older assemblages, whereas the *R. evoluta* fauna is already intermediate on the path to the *Reineckeia*-like genus *Xenostephanus* of the lower *A. mutabilis* Zone. (*b*) This conclusion has been confirmed by a short re-examination of Westbury pit, Wiltshire, by J. H. Callomon (1976, pers. comm.). An unusually low water-level revealed layers containing *R. evoluta* (M)+(m), 0–50 cm below a marker layer of septarian concretions, and *R. involuta* (M), 1 m below the concretions.

Horizon IV. R. (*Semirasenia*) *askepta* Ziegler, 1963 (M) and associated *R.* (*Rasenioides*) *lepidula* (Oppel) and spp. (m). Neither *R.* (*Zonovia*) nor *Xenostephanus* have so far been recorded from this horizon. The appearance of the fauna as a whole is that of small, fine-ribbed species which are difficult to distinguish when crushed from those of the *A. mutabilis* Zone above; the distinctions lie in the venter, which the secondary ribs cross without interruption in *Rasenia* but which shows a smooth band or groove in *Aulacostephanus* (see Ziegler 1963, p. 769). The boundary between the *R. cymodoce* Zone (top of fauna IV) and the base of the *A. mutabilis* Zone is therefore dictated largely by historical circumstance rather than striking faunal differences. Occurrence: (*a*) Eathie, Scotland (Ziegler 1963); (*b*) Westbury pit, Wiltshire, 2–3 m above the marker layer of septarian concretions as mentioned above; (*c*) Wyke Regis, Fleet shore, southernmost end, 100 m W. of boathouse at Small Mouth, with *R. askepta* and *R. lepidula* in clays.

In addition to these faunas there are yet others in museums awaiting clarification. One includes *R. similis* Spath, 1935 (p. 46, pl. 14, fig. 2 showing only the nucleus of a much larger specimen), a form developing the straight but irregular ribbing reminiscent of the 'degenerate' forms illustrated by Tornquist (1896) from Le Havre, Normandy. Another is the fauna of the Abbotsbury Ironstone, a ferruginous oolitic siltstone equivalent of the Kimmeridge Clay which occurs only some 10 km NW. of Wyke Regis (Brookfield 1973). It appears to contain at least the faunas of horizons II–IV.

The closest resemblance of the Andøya fauna is to that of horizon III, suggesting that the *R. evoluta* fauna from Andøya represents a level high in the *R. cymodoce* Zone.

It is more difficult to place the Andøya forms stratigraphically in relation to *Rasenia*-bearing beds of other northern localities, e.g. East Greenland and the U.S.S.R. In East Greenland Spath (1935, p. 74) subdivided the *Rasenia* beds of Milne Land into a lower horizon containing *R. orbignyi* Spath (*non* Tornquist) and a higher horizon containing *R. borealis* Spath. The latter was assigned to the *R. uralensis* Zone. All the material came from concretions of indurated siltstone. New collections made in 1957–1958 by Lauge Koch's expeditions (J. H. Callomon) and in 1968 (E. Håkansson, C. Heinberg) have shown, however, that these concretions occur in layers, of which there are at least four. Three successive faunas can be recognized: (*a*) a lower one with *R. orbignyi* Spath (*non* Tornquist) and ?*Pictonia* sp.; (*b*) one with typical *R. cymodoce* (d'Orbigny); and (*c*) one with *R. borealis* Spath, 1935 (holotype only, pl. 7), which has been rediscovered in association with typical *Aulacostephanus mutabilis* and is hence younger than any of the forms discussed here from the *R. cymodoce* Zone. The Andøya fauna is not included in any of these.

A subdivision of *Rasenia*-bearing horizons given by Mesechnikov from the Kheta River Basin (*in* Saks 1969) is not comparable with the horizons described from England, except that there also *R. orbignyi* (Tornquist) occurs in the lowermost part.

R. borealis (*non* Spath) *bojarkensis* Mesezhnikov may indicate the *R. uralensis* or *R. evoluta* horizon.

Taumholet Member. No ammonites were collected from the *c.* 150-m thick Taumhølet Member. The sandy facies of the Breisanden and Taumhølet members, together with the considerable thickness of the *R. evoluta* horizon, indicates a high rate of sedimentation. It is therefore probable that the Taumhølet Member still belongs to the Lower Kimmeridgian and that the Middle Kimmeridgian and the lower part of the Upper Kimmeridgian represent a period of non-deposition.

Ratjonna Member. The 100-m thick, silty Ratjønna Member can be referred to the Middle Volgian–Ryazanian. Ammonites from the lower part of the sequence, *Dorsoplanites* cf. *subpanderi* and *Pavlovia* (*Epipallasiceras*) cf. *pseudaperta*, are comparable with boreal Middle Volgian species. *D. subpanderi* occurs in the *P. rotunda–Progalbanites albani* zones of the Glauconitic Series of Milne Land, East Greenland (Spath 1936; Håkansson *et al.* 1971; Surlyk *et al.* 1973) and is also known from a similar level in Siberia (Mikhailov 1966). *Pavlovia* (*Epipallasiceras*) *pseudaperta* is found at one sharply defined level in the upper part of the Glauconitic Series of Milne Land (Callomon 1961). It occurs above faunas of *Pavlovia* that can be readily equated with those of the *P. rotunda* and *P. pallasioides* zones of England and hence in a similar position to the basal *Progalbanites albani* Zone of Dorset, which also yields the subgenus (Buckman 1926, pl. 693; as *Virgatites pallasianus* d'Orbigny, from Dorset, basal *P. albani* Zone; Callomon 1961; and Cope *et al.* 1969, p. A49). The subgenus *Epipallasiceras* was previously thought to be endemic to East Greenland.

The '*Virgatosphinctes*' sp. figured by Sokolov (1912, p. 10, pl. 1, fig. 6), which he himself compared to *Epivirgatites nikitini* (Michalski, 1890), was referred by Saks (1972, p. 96) to ?*Chetaites* sp. This genus occurs immediately below and above the Volgian–Ryazanian boundary in northern Siberia (see Basov *et al.* 1970) and is also known from the Upper Volgian of Greenland (Surlyk *et al.* 1973). The specimen may belong to a level in the Ratjønna Member not represented by ammonites in the collection described here.

The uppermost part of the Ratjønna Member contains *Surites* (*Bojarkia*) cf. *mesezhnikowi* and *Buchia volgensis*. *S.* (*B.*) *mesezhnikowi* characterizes the youngest zone of the Ryazanian in northern Siberia (Basov *et al.* 1970), which according to Casey (1973) can be correlated with the *Surites* (*Bojarkia*) *stenomphalus* and *Peregrinoceras albidum* zones of eastern England and with the upper part of the *S. spasskensis* Zone of the Russian platform (see also Saks 1972). *B. volgensis* was reported by Lahusen (1888) from the Ryazanian as well as from the Upper Volgian, but Upper Volgian representatives were not figured. Pavlov (1907) and most later Russian workers have indicated the species only from the lowermost Cretaceous. Jeletzky (1966, p. 33), moreover, stated that the Upper Volgian representatives may either belong to or be related to *B. richardsonensis* Jeletzky, 1966. However, new investigations seem to show that *B. volgensis* did have a long range. Thus, Zakharov (*in* Saks 1972) indicates *B. volgensis* from the Upper Volgian as well as from the Lower and Upper Berriasian of the Khatanga Depression, and in East Greenland (Wollaston Forland) where *Surites* (*Bojarkia*) and *B. volgensis* also occur together, *B. volgensis* has similarly been shown to have a long range (F. Surlyk, pers. comm. 1975). The

Upper Ryazanian *Surites* (*Bojarkia*)-*Buchia* level is also represented by identical or closely related species in eastern England (see Pavlov 1896; Casey 1973) and in Arctic Canada (see Jeletzky 1965, 1973).

Leira Member. The 50-m thick Leira Member of the Nybrua Formation, consisting of calcareous sandstones, siltstones, and marls, contains *B. keyserlingi s.l.* and ?*Neotollia* sp. in the lowermost part and ?*Thorsteinssonoceras* sp. in the upper part. Sokolov (1912) further mentions *Bochianites* cf. *neocomiensis* (d'Orbigny, 1842) in addition to belemnites and *Buchia* species that are not contained in the collection described here. *Buchia keyserlingi s.l.* has a wide circumpolar distribution in the Valanginian and ranges, at least in certain areas, from the Upper Ryazanian to the Upper Valanginian (Jeletzky 1965, 1973). *Neotollia* also has a circumpolar distribution, but is restricted to the Lower Valanginian (Saks 1972). *Thorsteinssonoceras* is known from Arctic Canada (Ellesmere Island) and Spitsbergen (Jeletzky 1965) and seems also to be restricted to the Lower Valanginian (Jeletzky 1973). An early Valanginian age for the Leira Member may thus be inferred.

Skarstein Formation. Apart from one poor fragment, identified as ?*Lytoceras* sp., the present collection contains no fossils from the Skarstein Formation. Spath (1947, p. 62) recorded the occurrence of a '*Crioceras*' sp. from these beds.

The Jurassic flora

Remains of plants occur throughout the sequence, but well-preserved macrofossils are confined to the bituminous shales of the Kullgrøfta Member, and to some sandstone layers of the Breisanden Member (text-fig. 2).

Fossil plants from these strata have been described by Heer (1877), Johansson (1920), Florin (1922), Bose (1959), and Manum (1968) (text-fig. 2). According to Manum (pers. comm.) the fossils from Andøya include seven or eight conifers, two ginkgophytes, one cycad, three bennettites, and two or three ferns, but Manum considers that the entire flora is in need of revision. Fragments of conifers dominate; especially common are leaves assigned to the genus *Sciadopitytes*. So far, none of the plants recorded have proved useful for detailed correlations with other areas.

The pollen and spores recorded in the Jurassic sequence on Andøya are characterized by long-ranging Mesozoic taxa (Vigran and Thusu 1975, table 2) and indicate the existence of a rich flora adjacent to the depositional basin. The abundance of biveciculate and araucariacean pollen, together with *Cerebropollenites mesozoicus*, *Concentrisporites hallei*, and *Perinopollenites elatoides*, suggest that a coniferous vegetation was dominant on Andøya.

The *Classopollis* complex (including *Corollina meyeriana*) in well-preserved assemblages never exceeds 1% of the identified species. Such rarity of *Classopollis* is recorded previously in Arctic Canada (Pocock 1970) and Siberia (Vakhrameev 1970). According to Hughes (1973) this rarity of *Classopollis* in the Arctic region, in contrast to its abundance in north-west Europe, may be a function of latitude.

Palynostratigraphy

Four palynological assemblages are recorded from the Jurassic and Cretaceous sequence. Only selected taxa from assemblages 1 and 4 are illustrated here. Readers should refer to Vigran and Thusu (1975, pls. 1–20, tables 2 and 3) for illustrations and complete lists of taxa with their stratigraphic distribution.

Assemblage 1. A rich, non-marine assemblage of pollen and spores is recorded from the Hestberget Member and, with reduced diversity, from the Kullgrøfta Member (Pl. 6). Although coniferous pollen grains dominate the assemblage, spores are strikingly well represented in the Hestberget Member. The onset of brackish conditions is recorded by the appearance of acritarchs (*Leiofusa jurassica*, *Metaleiofusa diagonalis*, *Micrhystridium* spp.) in the middle part of the Kullgrøfta Member.

The assemblage is assigned a Bajocian–Bathonian age because of its similarity with Scanian assemblages (Guy 1971; Mahin 1968; Tralau 1967, 1968; Tralau and Artursson 1972). Text-fig. 3 shows twenty-four selected taxa of which eighteen have been reported from other Scanian assemblages. Similar, but less diverse assemblages from the Netherlands have been reported by Herngreen and de Boer (1974). Comparison with British assemblages shows that *Foveotriletes microreticulatus* and *Leptolepidites equatibossus*, restricted respectively to the Bathonian and Bajocian in Britain (Couper 1958; Neves and Selley 1975), are present in Assemblage 1 together with *Clavatipollenites hughesii*, *Crybelosporites vectensis*, and *Kuylisporites lunaris*, which first appear in Britain in the Lower Cretaceous (Couper 1958; Kemp 1971).

In spite of the long-ranging nature of Jurassic palynomorphs and the strong sedimentary control over their distribution in north-west Europe, Assemblage 1 has proved useful for correlations of Middle Jurassic rocks from the Norwegian continental shelf.

Assemblage 2 is recorded from the Breisanden Member and in immediately over- and underlying beds (text-fig. 2). The Breisanden Member is placed in the *R. cymodoce* Zone of the Lower Kimmeridgian and contains dinocysts marking the onset of normal marine conditions on Andøya.

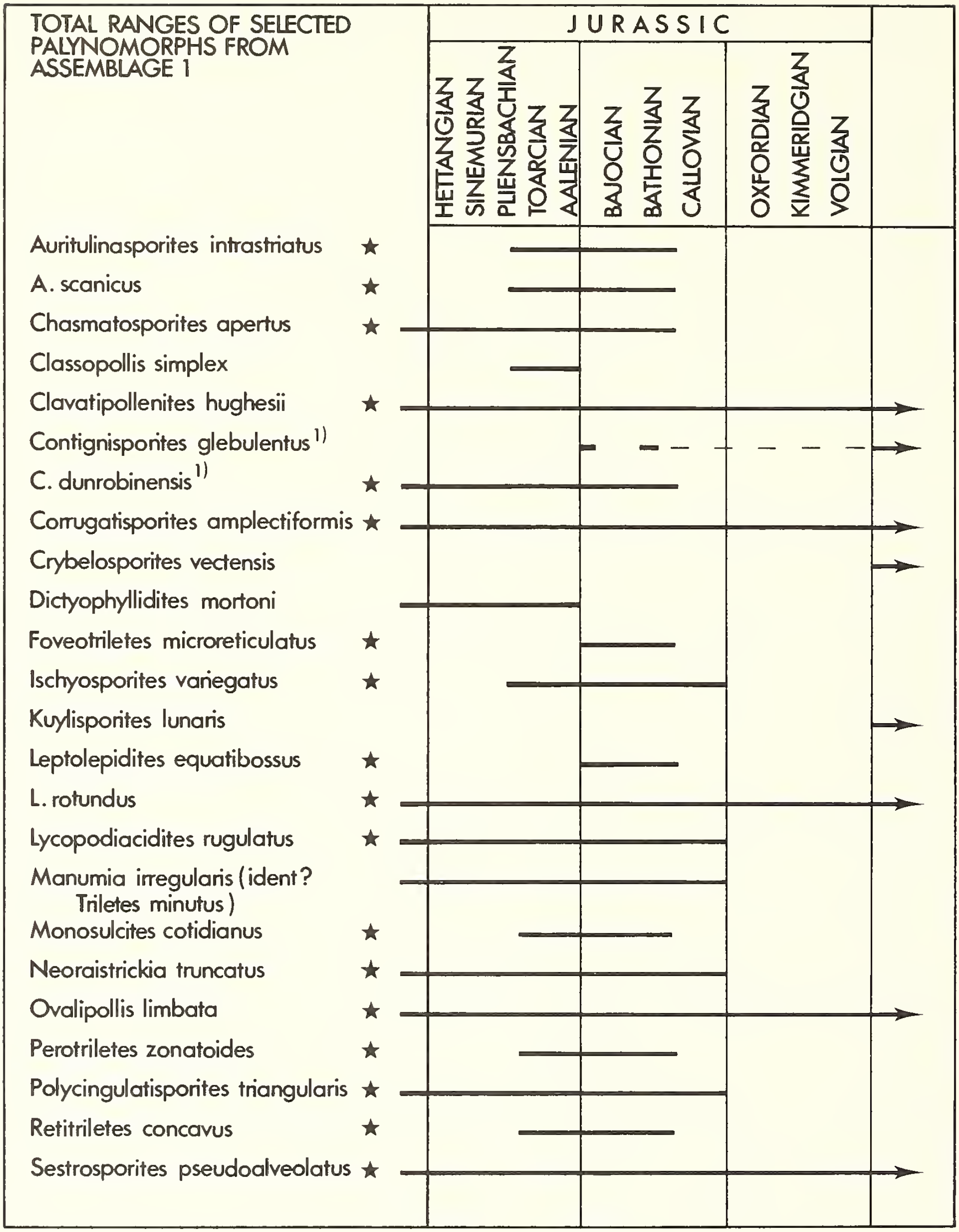
Many of the long-ranging spore and pollen taxa present in Assemblage 1 continue to dominate. A single diagnostic spore, *Cicatricosisporites sternum* Amerom, 1965 (*Schizaeoisporites heintzii* Bose, 1959) has been recorded. Dinocysts include *Gonyaulacysta jurassica*, *Cannosphaeropsis pulchra*, *Chlamydophorella wallala*, *Crassosphaera concinna*, *Oligosphaeridium anthophorum*, *O. dictyophorum*, *Scriniodinium crystallinum*, *Sirimiodinium grossi*, *Systematophora fasciculigera*, and *Systematophora* sp. (*Perisseiasphaeridium pannosum* of Vigran and Thusu, 1975). The assemblage is comparable with that reported by Neves and Selley (1975) from the Lower Kimmeridgian Allt-na-cuile Sandstone in north-east Scotland and also with assemblages from England (Gitmez 1970; Gitmez and Sarjeant 1972), although the Andøya assemblage shows lower diversity.

Assemblage 3 is restricted mainly to the lower and middle part of the Ratjønna Member (text-fig. 2). Most of the Taumhølet Member between assemblages 2 and 3 is essentially barren. The lower part of the Ratjønna Member, placed in the *Pavlovia rotunda*–*Progalbanites albani* zones of the boreal Middle Volgian, contains poorly preserved palynomorphs. Of note is *Classopollis echinatus*, which is also known from the 'higher Upper Malm' of the Netherlands (Burger 1966) and in the Upper Kimmeridgian and Portlandian of southern England (Norris 1969).

Dinocyst species, poorly preserved but fairly common, include *Gonyaulacysta* spp. (*G. cladophora*–*G. perforans* complex), *Dingodinium* sp. (*Netrelytron* cf. *stegastum* of Vigran and Thusu 1975), *Pareodinia ceratophora*, *Prolixosphaeridium granulosum*, and *Sirmiodinium grossi*. The assemblage differs from Assemblage 2 by the incoming of the *Gonyaulacysta* complex in abundance.

Assemblage 4. This is the youngest recorded assemblage (text-figs. 2, 4). The uppermost part of the Ratjønna Member, placed in the youngest Ryazanian ammonite Zone (*Surites* (*Bojarkia*) *mesezhnikovi*) contains a few dinocysts including *Pareodinia dasyforma* and *Oligosphaeridium complex*. *P. dasyforma*, a characteristic boreal form, is restricted to Neocomian strata on Spitsbergen (Bjærke *et al.* 1975), North Slope of Alaska (Wiggins 1975) and the Canadian Arctic (Pocock 1976); but this species has also been reported from the Kimmeridgian and Upper Volgian in England (Gitmez and Sarjeant 1972) and Russia (Vozzhennikova 1967). *O. complex* is cosmopolitan and ranges from the Valanginian to Middle Miocene. Since Upper Volgian strata are not represented in our sample collection, we tentatively suggest that *P. dasyforma* and *O. complex* appear for the first time in Ryazanian beds on Andøya.

The Lower Valanginian Leira Member of the Nybrua Formation contains *P. ceratophora*, *P. dasyforma*, *Mudrongia tetracantha*, *O. complex*, *Scrininiodinium apatelum*, *S. grossi* and *Systematophora* sp. Dating of the Skjermyrbekken Member on a megafaunal basis is lacking, but a late Valanginian age is



TEXT-FIG. 3. Total known ranges of selected palynomorphs from Assemblage 1, Andøya. [1] indicates probably conspecific taxa. * indicates palynomorphs reported from Bajocian–Bathonian assemblages in Scandinavia.

suggested by the presence of *Gardodinium trabeculosum*, *Pseudoceratium pelliferum*, and *Pterodinium magnoserratum*.

The Skarstein Formation lacks a megafauna, but sparse dinocysts include *Aptea polymorpha*, *Cyclonephelium distinctum*, and *Phoberocysta neocomica*. These are present in the lowermost beds of the Nordelva Member and indicate an early Cretaceous (Aptian?) age.

This assemblage is similar to those reported from other areas in north-west Europe and the Arctic, but some forms are largely dominant in boreal areas. Of note is the concurrence of *Pareodinia dasyforma* and *Scriniodinium* (? = *Tubotuberella*) *apatelum*. Both these species are abundant in Ryazanian sediments on Spitsbergen (Thusu, unpublished data) and are also reported in early Neocomian sediments from the North Slope of Alaska (Wiggins 1975 and unpublished data from the Jurassic-Cretaceous Boundary Circular). Furthermore, Vozzhennikova (1967) reports *P. dasyforma* and species of *Tubotuberella* from the Upper Volgian of the Moscow Basin. These occurrences suggest close links of dinocyst assemblages in boreal areas.

The Jurassic of Trondelag

The glacial erratics of sideritic ironstone and coal, which were collected along Trondheimsfjord, are non-marine deposits with fossil plants. A Middle Jurassic age for these deposits is suggested by a small collection of leaf cuticles which are related to the Middle Jurassic flora of Yorkshire (Vigran 1970). Palynomorphs from the same rocks include the following important taxa also present in Assemblage 1 of Andøya: *Chasmatosporites apertus*, *Clavatipollenites hughesii*, *Contignisporites glebulentus*, *Corrugatisporites amplectiformis*, *Crybelosporites vectensis*, *Dictyophyllidites mortonii*, *Foveotriletes microreticulatus*, *Gleicheniidites granulatus*, *Ischyosporites variegatus*, *Kuylisporites lunaris*, *Leptolepidites equatibossus*, *Lycopodiacidites rugulatus*, *Monosulcites cotidianus*, *Neoraistrickia truncatus*, *Ovalipollis limbata*, *Polycingulatisporites triangularis*, and *Retitriletes concavus*.

The dominance of the *Cycadopites* complex together with the coniferous pollen grains is in marked contrast to Andøya where conifers are singularly dominant. The *Classopollis* complex is infrequent as on Andøya.

Calcareous sandstones, dated as Middle Jurassic from the associated fauna (Nagy *in* Thusu and Vigran 1975), were collected off the coast of Trøndelag (Oftedahl 1975). The assemblage contains the following taxa which are common with Assemblage 1: *Contignisporites glebulentus*, *Corrugatisporites amplectiformis*, *Crybelosporites vectensis*, *Ischyosporites variegatus*, *Neoraistrickia truncatus*, and spore sp. A.

Furthermore, the assemblage is characterized by the presence of typical Middle Jurassic dinoflagellates including *Chytroeisphaeridia chytroeides*, *C.* cf. *pococki*, *Gonyaulacysta* sp., *Nannoceratopsis gracilis*, *Pareodinia ceratophora*, and *Valensiella ovulum* (as *V. ovalum in* Vigran and Thusu 1975). This assemblage is similar to the Bajocian assemblage recorded from the North Sea (Thusu and Vigran 1975).

Core and grab samples recovered from Haltenbanken (Thusu and Vigran 1975), and from deposits south of Trøndelag (unpublished data), contain the following species: *Acanthotriletes varispinosus*, *Chasmatosporites* sp. cf. *C. major*, *Corrugatisporites amlectiformis*, *Foveosporites canalis*, *Ischyosporites variegatus*, *Kuylisporites lunaris* and spore sp. A. This assemblage, although reduced, is similar to Assemblage 1 of Andøya.

CONCLUSIONS

The stratigraphy established here allows comparison of the geological evolution of the Andøya basin with other marginal areas of the northernmost Atlantic Ocean.

The Middle Jurassic faulting, and initiation of deposition of non-marine Bajocian-Bathonian sediments is contemporaneous with widespread transgressions across the marginal areas of East Greenland (Birkelund 1975) and Spitsbergen (Parker 1967). At the same time the northern North Sea was marked by the 'Great Estuarine' regression causing separation of the 'Tethyan' and Boreal Seas (see Callomon 1975).

In Scotland transgressive pulses occurred in Callovian and Oxfordian times and further deepening apparently took place during the early Kimmeridgian (Sykes 1975). East Greenland is also characterized by Callovian and Oxfordian transgressions, and in late Oxfordian-early Kimmeridgian time marked subsidence occurred. The Lower Kimmeridgian transgression of Andøya may be related to the widespread subsidence of the North Atlantic area, marked by widespread unconformities and facies changes.

The late Kimmerian phase of faulting in late Jurassic-early Cretaceous time, prominent over the whole northern Atlantic area, is indicated by an unconformity at the Ryazanian-Valanginian boundary (between Dragneset and Nybrua formations) in the Andøya sequence, while sedimentation appears to be continuous across the Jurassic-Cretaceous boundary.

Boreal Bajocian-Bathonian ammonites are not known south of the Shetlands (Callomon 1975). As a consequence of the Callovian transgression the sharp faunal break disappeared during the late Jurassic, but boreal elements were still persistent. This is demonstrated by the known southernmost extension of ammonite taxa from Andøya as far as Dorset, England.

Four diagnostic assemblages of palynomorphs are reported from Andøya. Non-marine, spore and pollen Assemblage 1 of Bajocian-Bathonian age shows close resemblance to those from the Middle Jurassic of Trøndelag, Haltenbanken, Sweden

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TEXT-FIG. 4. Selected taxa from dinocyst Assemblage 4, Lower Cretaceous, Andøya.

1, *Pareodinia dasyforma* Wiggins, 1975. Specimen illustrating distal bifurcation of processes, ×650. Sample E-18, slide 75-23/5, co-ord. 23·2-103. Nybrua Formation, Leira Member.

2, *Gonyaulacysta serrata* (Cookson and Eisenack) Sarjeant, 1969. Specimen showing helicoid cingulum and a short, blunt, apical prominence, ×400. Sample F-21, slide 76-26/1, co-ord. 16·8-98·6. Skarstein Formation, Nordelva Member.

3, *Phoberocysta neocomica* (Gocht) Millioud, 1969. Complete specimen with operculum, ×400. Sample E-11, slide E-11/5, co-ord. 32-112. Nybrua Formation, Leira Member.

4, *Cyclonephelium distinctum* Deflandre and Cookson, 1955. Specimen illustrating a bald central part, processes confined to periphery, ×750. Sample F-21, slide F-21/1, co-ord. 47·6-98. Skarstein Formation, Nordelva Member.

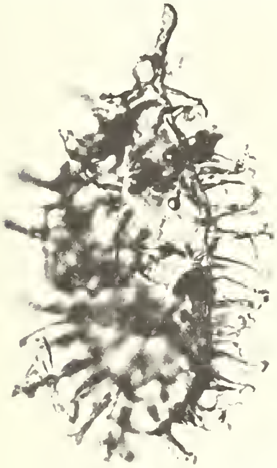
5, *Muderongia tetracantha* (Gocht) Alberti, 1961. Specimen without operculum, ventral view, ×350. Sample F-21, slide 75-26/6, co-ord. 42·8-111·2. Skarstein Formation, Nordelva Member.

6, *Scriniodinium apatelum* Cookson and Eisenack, 1960. Specimen illustrating elongated tubular antapical pericoel, ×650. Sample E-18, slide 75-23/2, co-ord. 14·9-101·9. Nybrua Formation, Leira Member.

7, *Pterodinium magnoserratum* Cookson and Eisenack, 1962. Specimen illustrating fields bordered by relatively high, coarsely serrated wing-like membrane, ×600. Sample F-19, slide F-19/1, co-ord. 43-112·6. Nybrua Formation, Skjermyrbekken Member.

8, *Sirmiodinium grossi* (Alberti) Warren, 1973. Specimen showing surface features and cingulum, dorsal view, ×450. Sample E-13, slide 75-22/4, co-ord. 21·5-111·4. Nybrua Formation, Leira Member.

and the Netherlands; however, there are certain differences, mainly involving the ranges of taxa, in comparison with Middle Jurassic assemblages from Great Britain. The rarity of the *Classopollis* complex in Andøya and Trøndelag agrees with similar records from Arctic Canada and Siberia. Marine dinocyst Assemblages 2 and 3 of Upper Jurassic age, and Assemblage 4 of Neocomian age, although showing a lower diversity are comparable with those reported from other areas in north-west Europe and the Arctic. The presence of *Pareodinia dasyforma* together with *Scriniodinium* (? = *Tubotuberella*) *apatelum* in Assemblage 4 on Andøya suggests closer links with boreal dinocyst assemblages from Spitsbergen, the Moscow Basin, and the North Slope of Alaska. However, further detailed regional investigation will be the subject of a future publication.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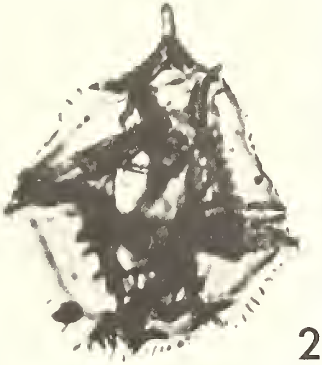
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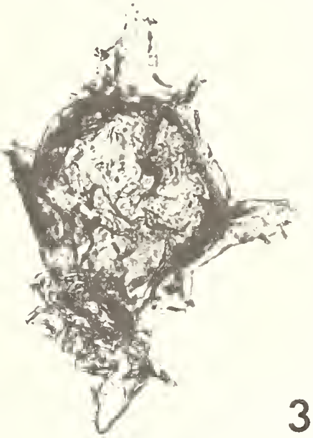
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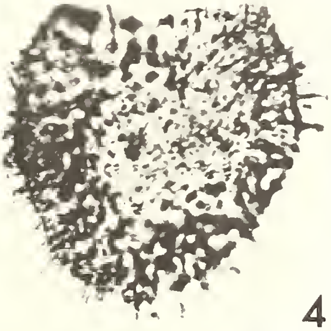
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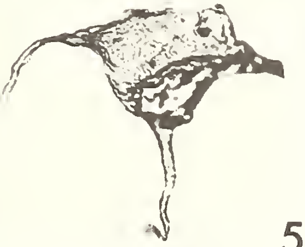
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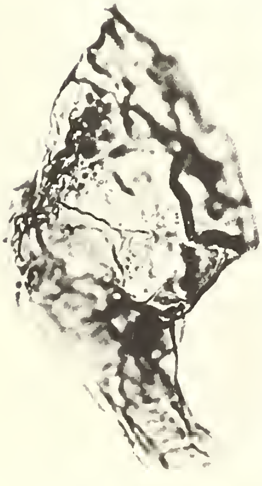
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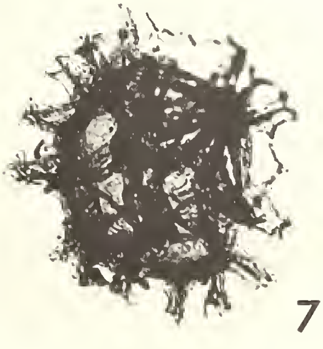
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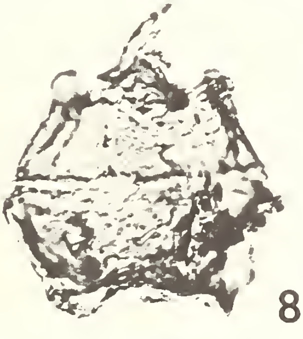
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SYSTEMATIC DESCRIPTIONS

Unless otherwise indicated, all figured specimens are in Paleontologisk Museum, University of Oslo.

Genus AMOEBOCERAS Hyatt, 1900
Amoeboceras (*Amoebites*) sp.

Plate 1, fig. 6

?1912 *Cardioceras alternans* v. Buch; Sokolov, p. 6.
?1953 *Amoeboceras* (*Amoebites*) sp.; Ørvig, p. 20.

Material. Two specimens from level A-103, two from level A-104, and two from level A-106, Breisanden Member of Dragneset Formation.

Remarks. Sokolov's (1912) report of *Cardioceras alternans* and Ørvig's (1953) record of an *Amoeboceras* (*Amoebites*) species from Andøya may refer to this species. The specimens appear to belong to the *A.* (*A.*) *kitchini* group, but specific determination is not possible because of the poor preservation.

Genus RASENIA Salfeld, 1913
Subgenus ZONOVIA Sazonov, 1960
Rasenia (*Zonovia*) *evoluta* Spath, 1935

Plate 1, figs. 4, 5; Plate 2, figs. 7–10; Plate 3, figs. 1–5; text-figs. 5, 6

1953 *Rasenia* sp.; Ørvig, p. 19.

Lectotype. BM 39801, a syntype in the British Museum (see below) is here designated lectotype (text-fig. 5*a*, *b*). Maximum diameter 59·7 mm. At 58·6 mm diameter, whorl height = 19·1 mm, whorl breadth = 21·9 mm, umbilical width = 25·2 mm. On the outer whorl at 60 mm diameter there are twenty-two primary ribs, and about sixty-eight ribs cross the venter. The specimen is a fully septate phragmocone of a macroconch.

Locus typicus. Brigg, Lincolnshire.

Stratum typicum. Lower Kimmeridgian, *R. cymodoce* Zone, upper part.

Material. Numerous poorly preserved internal casts of *Rasenia* occur in the Breisanden Member of the Dragneset Formation (C-32:1; C-33:7; C-34:6; C-36:55; A-103:2; A-104:2; A-105:6; A-106:1).

Description. The material from Andøya consists mostly of fragmentary phragmocones ranging in diameter from 50 to 150 mm, but also contains large specimens, up to

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EXPLANATION OF PLATE 1

Figs. 1, 2. *Pavlovia* (*Epipallasiceras*) cf. *pseudaperta* Spath. Casts of external moulds. Dragneset Formation, Ratjønna Member. 1, level D-144. 2, level D-150.

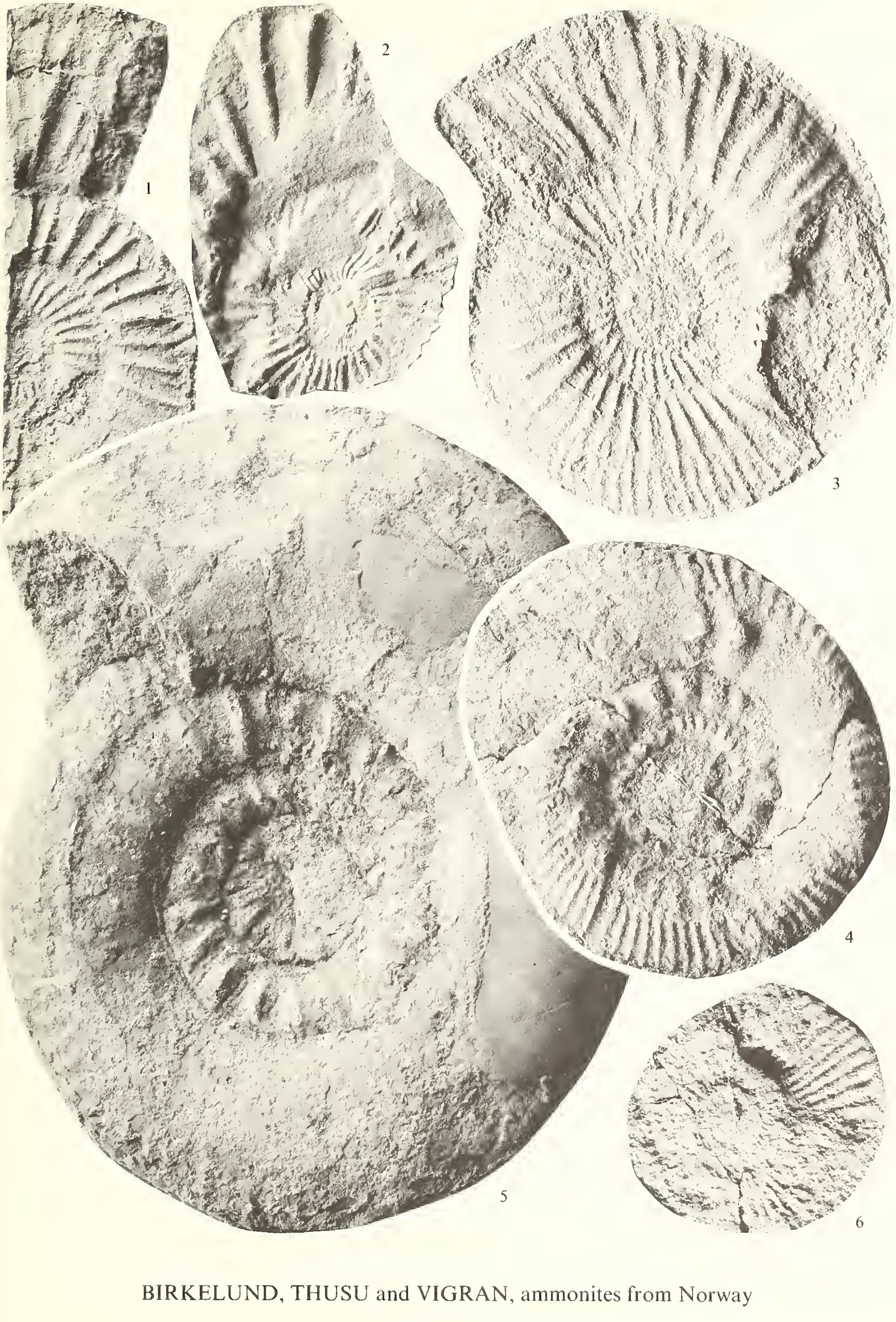
Fig. 3. *Dorsoplanites* cf. *subpanderi* Spath. Cast of external mould. Dragneset Formation, Ratjønna Member, level D-138.

Figs. 4, 5. *Rasenia* (*Zonovia*) *evoluta* Spath (M). Crushed internal casts, parts of shell preserved in 5. Dragneset Formation, Breisanden Member, level C-36.

Fig. 6. *Amoeboceras* (*Amoebites*) sp. Crushed internal cast. Dragneset Formation, Breisanden Member, level A-104.

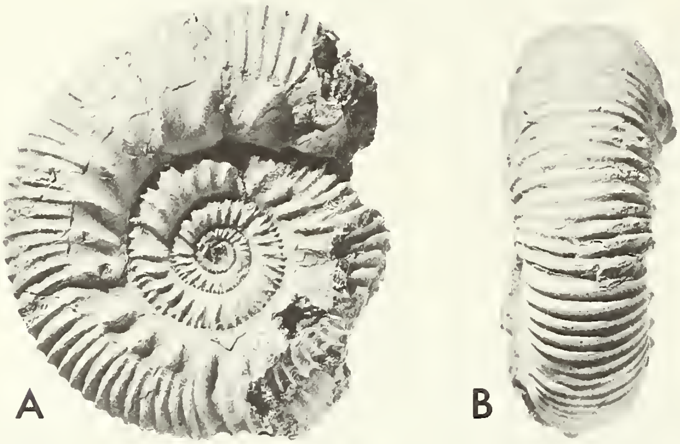
All × 1.

PLATE 1



BIRKELUND, THUSU and VIGRAN, ammonites from Norway

250 mm in diameter, with the greater part of the body chamber preserved. Nearly all specimens are badly crushed and only one side is preserved. The umbilicus ranges from 42 to 49% of the shell diameter in nineteen specimens. The umbilical ratio shows no obvious ontogenetic or stratigraphic variation. However, the measurements should be viewed with reservation because the specimens are crushed.

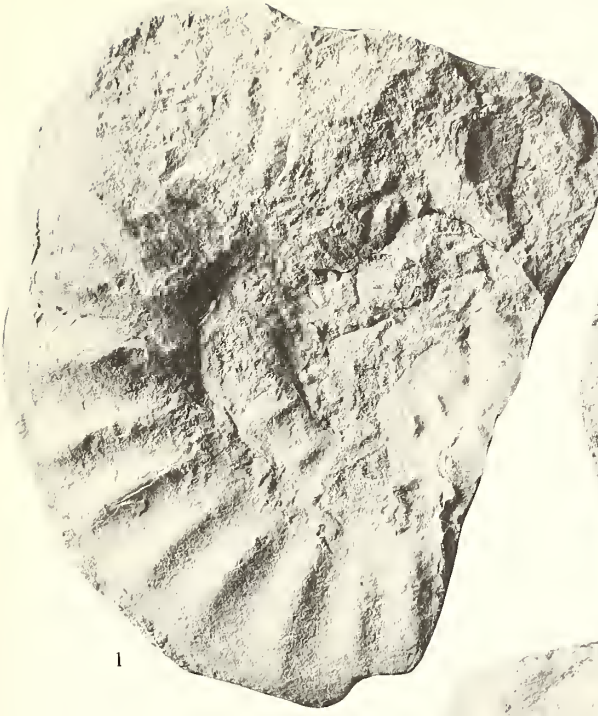


TEXT-FIG. 5. *Rasenia* (*Zonovia*) *evoluta* Spath (M), lateral and ventral view of nucleus, lectotype, BM 39801. Brigg, Lincolnshire, ×1.

The sculpture of the innermost whorls is poorly preserved. From a shell diameter of *c*. 30 mm a rasenid ribbing pattern can be seen. The primary ribs are usually very strong and bullate. The relationship between primaries and secondaries is 1:3–4, but in certain cases the primaries are very irregularly developed and may be completely missing on parts of the shell; in such cases counts of primaries and secondaries become meaningless (Pl. 1, fig. 4). The secondaries appear to pass over the venter without interruption. The ornament disappears at very variable diameters, usually between 110 and 130 mm. In some specimens the primaries disappear before the secondaries, in other specimens it is the opposite, and in still others both primaries and secondaries become reduced simultaneously. Most specimens are completely smooth for $\frac{1}{2}$–$\frac{3}{4}$ whorl before sculpture reappears as straight, blunt single, or occasionally bifurcate ribs.

EXPLANATION OF PLATE 2

Figs. 1–4. *Rasenia* (*Zonovia*) *evoluta* Spath (M). Crushed internal casts. Dragneset Formation, Breisanden Member. 1, level A-105, ×0·5. 2, level C-36, ×1. 3, level C-36, ×1. 4, level C-31, ×0·5.



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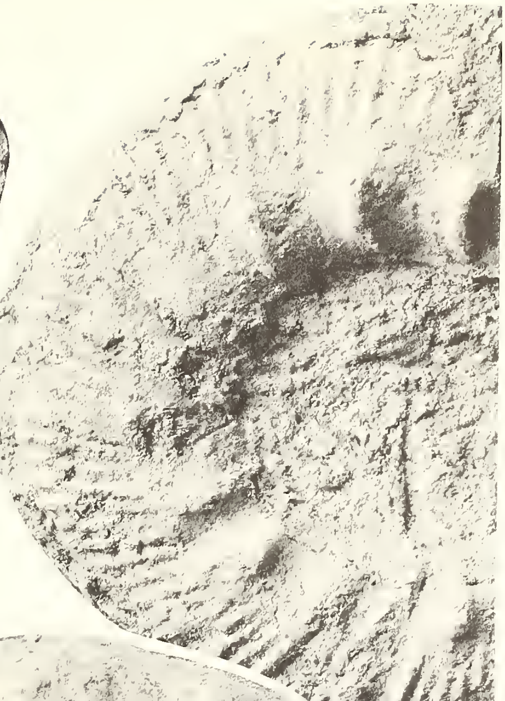

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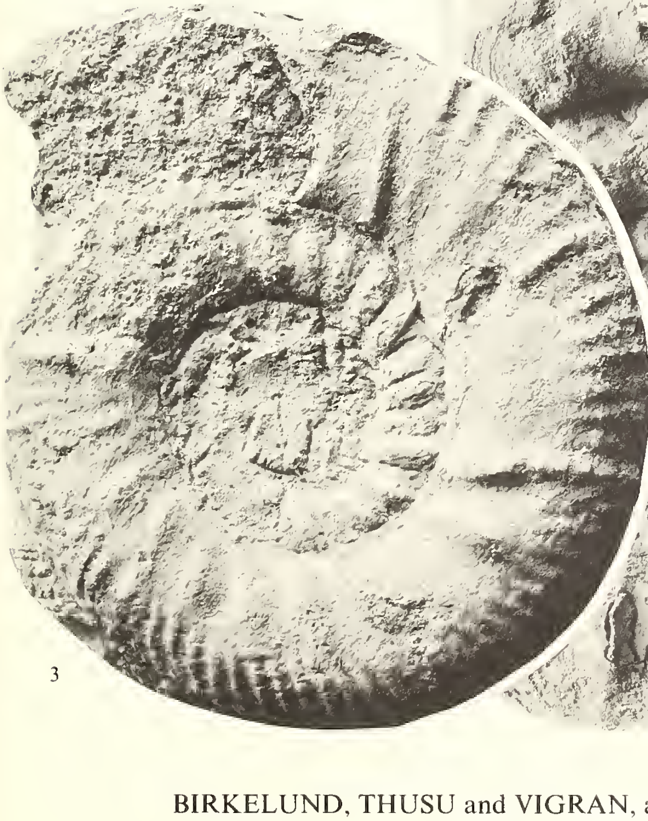

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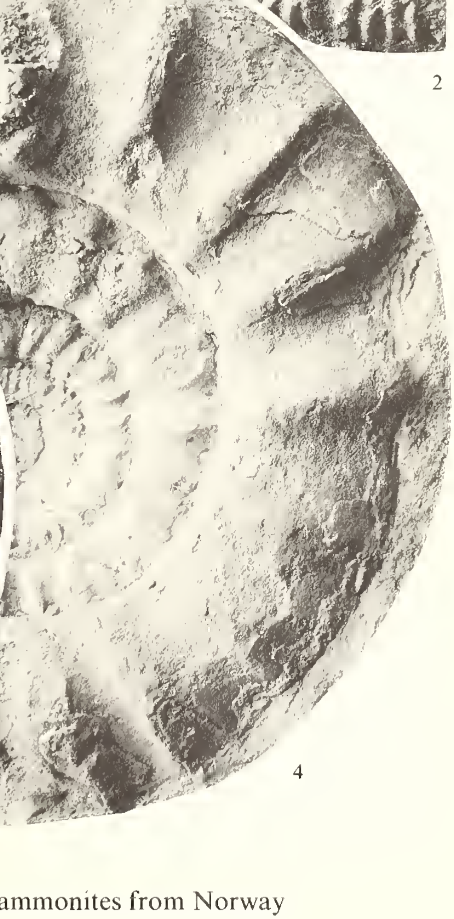

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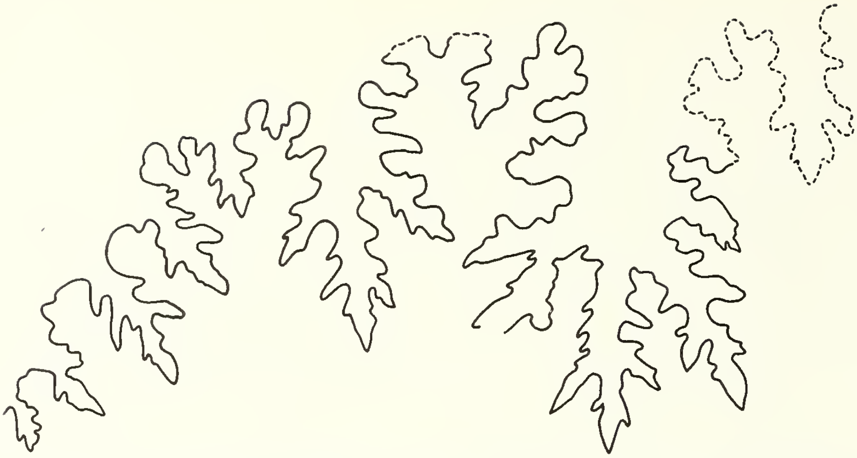
BIRKELUND, THUSU and VIGRAN, ammonites from Norway



TEXT-FIG. 6. Suture-line of *Rasenia* (*Zonovia*) *evoluta* Spath. Dragneset Formation, Breisanden Member, level C-36, × 3.

Sutures are occasionally preserved and show a rather finely incised pattern (text-fig. 6).

Discussion. The *Rasenia* species from Andøya shows a strong resemblance to a species from Market Rasen, referred to *R. uralensis* (d'Orbigny, 1845) or to *R. evoluta* by Salfeld (1913, 1914, MS), Spath (1935), and others.

The *Rasenia* species from Market Rasen have never been properly described. According to Spath (1935, p. 48) the fauna contains *R. uralensis* (d'Orbigny, 1845), *R. involuta*, and *R. evoluta* (Salfeld MS) Spath, 1935, and a number of undescribed species, some of which are perfectly smooth while others resemble *R. borealis* Spath, 1935 from East Greenland. In addition Spath (1935, p. 46, pl. 14, fig. 2*a*, *b*) established a *R. similis* on the basis of material found in drift at Norton Wood, Norfolk.

Study of material in the British Museum (Natural History), Institute of Geological Sciences, London, and Sedgwick Museum (Cambridge) allows the following brief descriptions to be made:

(*a*) *Rasenia uralensis* (d'Orbigny, 1845): The largest specimen figured by d'Orbigny (1845, pl. 32, figs. 6, 7, 10) was designated lectotype of *R. uralensis* by Salfeld (1913, p. 429), but is now presumed lost. A smaller syntype was figured by Douvillé (1911,

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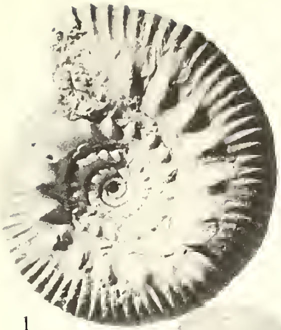
EXPLANATION OF PLATE 3

Figs. 1–3. *Rasenia* (*Zonovia*) *evoluta* Spath? 1, 2, (M), lateral and ventral view of nucleus, SM J29109, × 1. 3, (m), SM J29115, × 1.

Figs. 4, 5. *Rasenia* (*Zonovia*) *evoluta* Spath. 4, (M), fully grown, SM J62725, × 0·5. 5, (M), nucleus, SM J29090, × 1.

Fig. 6. *Rasenia* (*Eurasenia*) *involuta* Spath (M), with part of body chamber preserved, SM J29081, × 1.

All specimens from Market Rasen, Lincolnshire, housed in the Sedgwick Museum, Cambridge.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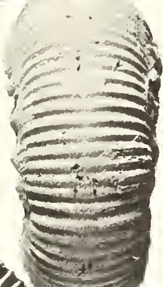
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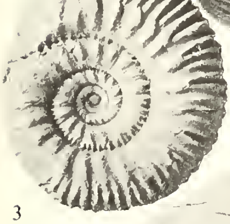
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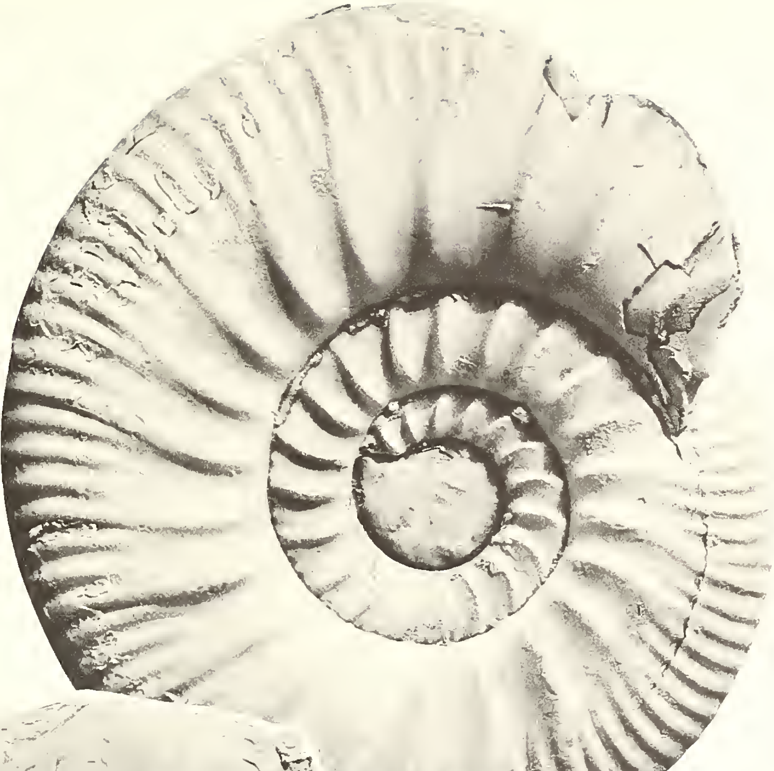
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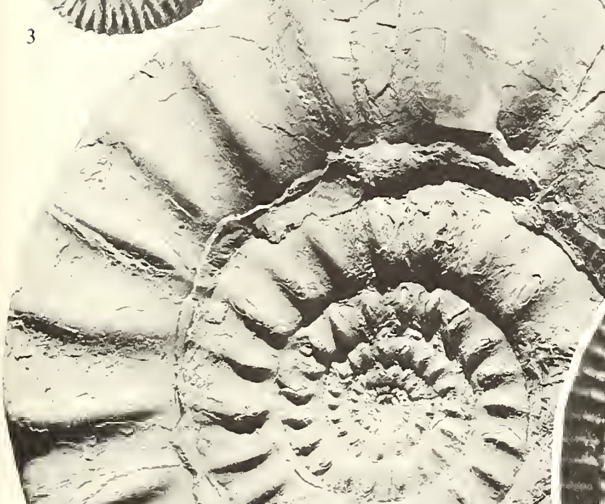
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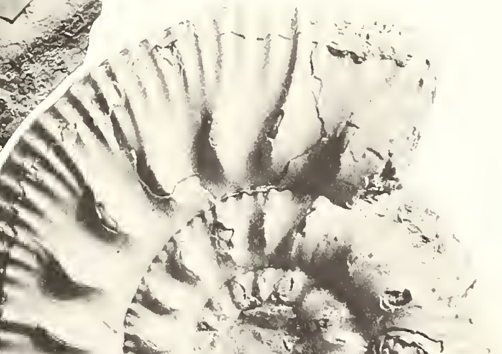
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BIRKELUND, THUSU and VIGRAN, *Rasenia* from Norway pl. 210^{a}, figs. C^{1}, C^{1A}), and designated as 'lectotype' by Ziegler (1962, p. 26). This specimen was collected by de Verneuil in Russia (Kineshima on the Volga) and formed part of d'Orbigny's type material; it appears to accord fairly well with the larger lectotype figured by d'Orbigny. It shows the moderately evolute inner whorls (umbilical ratio 42%) with depressed whorl section and rather strong bullate primaries. The relation between primaries and secondaries on the last whorl preserved is 1:4. The secondaries seem to cross the venter uninterruptedly although they may be slightly weaker on that part of the shell. Outer whorls and body chamber are not known from type material.

Many septate nuclei from Market Rasen, fauna **B**, are rather similar to the lectotype and the syntype figured by Douvillé, but are generally more evolute and less inflated; the primary ribs are more coarse, and the fasciculate secondary ribbing of the inner whorls is usually clearly exposed in the umbilicus. The Market Rasen specimens are therefore here referred to *R. evoluta* Spath (see below).

(*b*) *Rasenia evoluta* Spath, 1935: This species, used as a manuscript name by Salfeld, was formalized by Spath (1935, pp. 48–49). Spath stated that *R. evoluta* was a large species, but figured only a small, wholly septate, and barely interpretable nucleus (1935, pl. 14, fig. 6*a*, *b*; BM C8046). This specimen was therefore considered as the holotype by Arkell and Callomon (1963, p. 223). Because of its close similarity to the lectotype of *R. involuta* Spath, 1935 the name *R. evoluta* was placed in subjective synonymy by these authors.

Since then it has become clear that the type series of *R. evoluta* must be regarded as more extensive than previously thought, and hence that there is no holotype. Following Spath's description the types must include at least all the specimens labelled *R. evoluta* by Salfeld in the British Museum. Besides the small nucleus figured in 1935, there is one other specimen (M. K. Howarth pers. comm.). It is also a wholly septate nucleus, 60 mm in diameter, but determinable, for it closely resembles other, abundant nuclei at similar diameters in collections from Market Rasen, fauna **B**, in which the ontogeny can be reconstructed up to the final adult stage of what is clearly a macroconch. Spath's reference to large specimens suggests that the type series of his species includes additional specimens, but labels in his handwriting may not be reliable evidence as they could include metatypes (topotypes subsequently identified by the original author).

To settle this problem finally and at the same time to attach a firm name to the Market Rasen fauna **B**, the second syntype of *R. evoluta*, BM 39801, is now designated lectotype. It is illustrated in text-fig. 5. In the adult, as is usual in perisphinctid macroconchs, the last whorl or so shows a wide range of variation in ribbing, which may disappear completely and reappear again as straight, blunt single or bifurcating ribs. Five complete, mature specimens in the Sedgwick Museum range from 150 to 220 mm in diameter. One of these is shown in Plate 3, fig. 4.

(*c*) *Rasenia involuta* Spath, 1935 (p. 48, pl. 10, fig. 5*a*, *b*): Arkell and Callomon (1963, p. 221) pointed out that the lectotype (BM 50629b) is a nearly complete specimen and that it seems to be a microconch, as the body chamber gives the impression near the end of slight contraction indicating maturity. The specimen is slightly more involute than the type of *R. uralensis* and the whorls are more compressed. It is considerably more involute than *R. evoluta*, and a number of similar microconchs in the collections bear out the point to which Spath drew attention, that in *R. involuta* the secondary ribs on the inner whorls are always covered and hence not visible in the umbilicus. In addition, the collections contain many macroconchs in the Market Rasen fauna A, almost all juveniles having some body chamber preserved, in which the whorl section of the intermediate whorls becomes notably compressed and oval, and the primary ribbing becomes subdued and only moderately flexuous, not strongly bullate, most of the secondaries being intercalatories (Pl. 3, fig. 6). These specimens are here considered to be the macroconchs of *R. involuta*. A subgeneric name for them could be *Eurasenia* Geyer, 1961 (type species *R. rolandi* (Oppel 1863)).

(*d*) *Rasenia similis* Spath, 1935 (p. 46, pl. 14, fig. 2*a*, *b*): Spath figured only the inner whorls of the holotype, although outer whorls are partly preserved (BM C36504). The specimen is almost as involute as *R. involuta* macroconchs and is also similar to *R. involuta* in cross-section of the whorls. It differs in having straighter, non-bullate primary ribs that branch indistinctly and irregularly, with many intercalatories, as in *Pictonia normandiana* Tornquist (1896, p. 20, pl. 5, fig. 1; pl. 6, fig. 2) from the *P. baylei* Zone of Normandy. Although Spath thought it transitional between *R. cymodoce* and the *R. uralensis* group, it might in fact be earlier than either, transitional even between *Pictonia* and *Rasenia*. Another specimen, in the Institute of Geological Sciences (No. 30740), is still septate at a diameter of 18 cm. Both specimens are from glacial drift, so nothing can be said about their precise ages.

Among the Market Rasen species the Andøya material is clearly most closely related to *R. evoluta*, from which it seems to differ only in a more irregular spacing of the primary ribs, and in being slightly more involute. Typical *R. evoluta* is also known from glacial erratics in northern Jutland.

The Andøya material has also been compared with the *R. cymodoce* group as described by Spath from Milne Land, East Greenland (Spath 1935) under the name *R. orbignyi* (Tornquist, 1896) and varieties.

R. orbignyi Spath (*non* Tornquist) shows an extremely wide range of variation, both in umbilical ratio and in ornamentation, but this may be due in part to slight differences in age. The species is similar to the material from Andøya in umbilical ratio (38–50%) and in the disappearance of ribbing on later parts of the shell. Also the wide variation in the degeneration of the ribs on the outer whorls is similar. However, it seems to differ in having a smaller size and weaker and straighter primaries. *R. borealis* Spath, 1935, as represented by the holotype, is from a higher level than *R. orbignyi* in Milne Land. It is similar to the Andøya material in size and the style of ribbing on the mature body chamber, but differs in the inner whorls, which are very evolute and densely ribbed with straight primaries that furcate visibly in the umbilicus, rather as in *Aulacostephanus*, and suggest affinity with *A.* (?) (*Xenostephanoides*?) *groenlandicus* Ravn, 1911 (pl. 37, fig. 3*a*–*c*, from Store Koldewey; and Frebold 1930, pl. 9, figs. 3, 4; pl. 22, fig. 2), as already suggested by Spath.

Genus DORSOPLANITES Semenov, 1898
Dorsoplanites cf. *subpanderi* Spath, 1936

Plate 1, fig. 3

1936 *Dorsoplanites subpanderi* Spath, p. 76, pl. 27, fig. 5*a*, *b*; pl. 31, fig. 1*a*, *b* (holotype).
1966 *Dorsoplanites subpanderi* Spath; Mikhailov, p. 28, pl. 6, fig. 3; text-fig. 10.

Material. Two specimens from level D-138, Ratjønna Member of Dragneset Formation.

Remarks. The figured specimen is close to *Dorsoplanites subpanderi* Spath in coiling and ribbing pattern, with the ribs fairly regularly bifurcate as in that species. The ribs differ in having slightly closer spacing and the primaries may be less blunt, being more similar to *D. jamesoni* Spath (1936, pl. 29, fig. 3; pl. 30, fig. 1) in these characters. However, *D. jamesoni* differs distinctly in having a greater number of single ribs, especially near the aperture.

The figured specimen shows a change in ribbing pattern close to the aperture as seen in other representatives of this genus. A final specific determination is not possible because of the poorly preserved cross-section.

Genus PAVLOVIA Ilovaisky, 1917
Pavlovia (*Epipallasiceras*) cf. *pseudaperta* Spath, 1936

Plate 1, figs. 1, 2

1936 *Pavlovia* (*Epipallasiceras*) *pseudaperta* Spath, p. 56, pl. 8, fig. 1; pl. 9, figs. 3, 4; pl. 11, fig. 5; pl. 16, figs. 1 (holotype), 4; pl. 20, fig. 1; pl. 39, fig. 2.

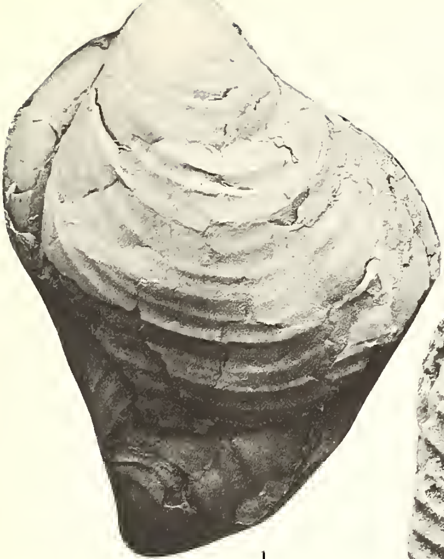
Material. One specimen from level D-144 and one from level D-150. In addition a number of fragments, mostly nuclei, from levels D-144, D-145, D-149, and D-150, which may belong to the same subgenus. Ratjønna Member of Dragneset Formation.

Remarks. The subgenus *Epipallasiceras* contains among the most easily recognizable of the enormous spectrum of forms included in the genus *Pavlovia.* The characteristic features are the densely and finely ribbed involute inner whorls, shared with *P.* (*Pallasiceras*), flat whorl sides, straight, sharp regular primary ribs bifurcating high on the whorl side into almost equally strong and sharp closely spaced secondaries just exposed in the umbilicus, all illustrated in Plate 1, fig. 1. The Andøya forms are very similar to the holotype of *P.* (*E.*) *pseudaperta* itself, but the crushing makes definite identification impossible.

EXPLANATION OF PLATE 4

Figs. 1, 2. *Buchia volgensis* (Lahusen). Left valve, and posterior view, × 1.
Figs. 3, 4. *Surites* (*Bojarkia*) cf. *mesezhnikowi* (Shulgina). Crushed internal casts preserved together with fragmentary *Buchia volgensis*, × 1.

All from Dragneset Formation, Ratjønna Member, level D-164.



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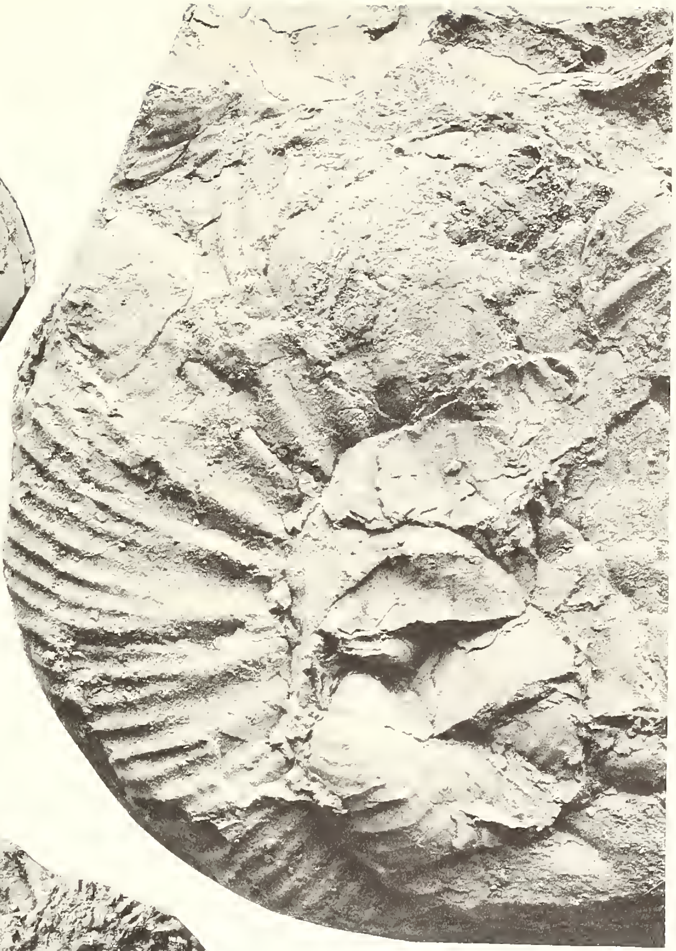

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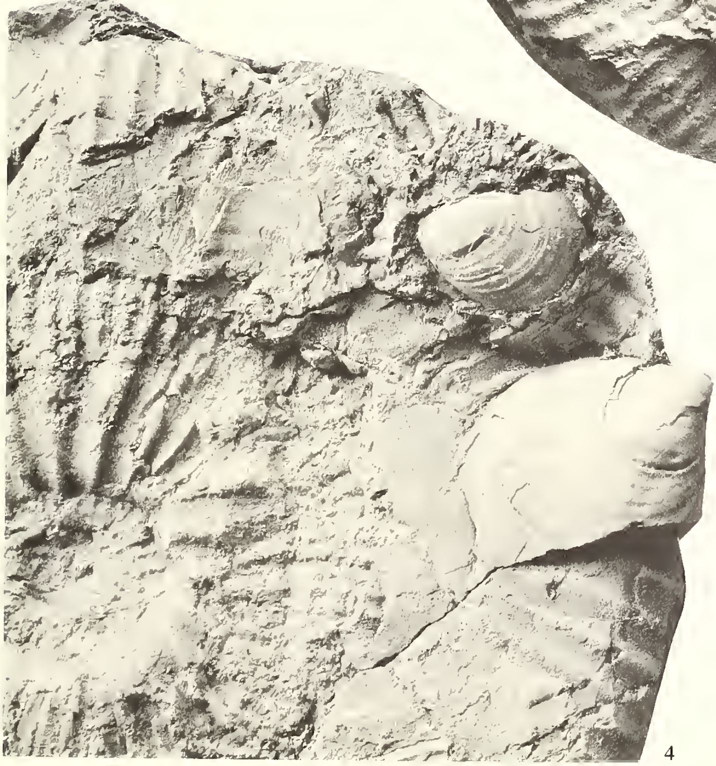

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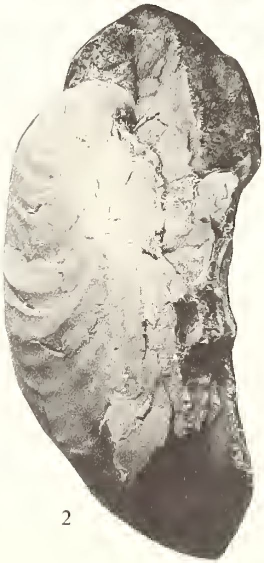

2

BIRKELUND, THUSU and VIGRAN, ammonites and bivalves from Norway

Genus SURITES Sazonov, 1951

Surites (*Bojarkia*) cf. *mesezhnikowi* (Shulgina, 1969)

Plate 4, figs. 3, 4; Plate 5, fig. 1

1969 *Bojarkia mesezhnikowi* Shulgina *in* Saks and Shulgina, p. 46, pl. 1, figs. 1 (holotype), 2, 3.
1972 *Bojarkia mesezhnikowi* Shulgina; Shulgina *in* Saks, p. 158, pl. 14, figs. 1, 2.

Material. Five crushed specimens from level D-164, Dragneset Formation, Ratjønna Member.

Remarks. The specimens show a very narrow range of variation. All are rather involute, the umbilical ratio being about 30% at a shell diameter of 9 cm (Pl. 5, fig. 1). The ribbing changes from a fine to a considerably coarser pattern at a diameter of about 2 cm. From a diameter of 8 cm to 10 cm trifurcating ribs or bifurcating ribs with one intercalatory rib dominate. After branching the ribs bend slightly backwards, and towards the ventral side they seem to bend slightly forwards. From a diameter of about 10 cm further secondaries are intercalated. On the outermost whorl preserved of the wholly septate specimens the sides become smooth, while secondaries are preserved on the ventral side.

The specimens are similar to *Surites* (*Bojarkia*) *mesezhnikowi*, which also seems to grow large and somewhat smooth. According to Casey (1973, pp. 250–252) *S.* (*B.*) *mesezhnikowi* is very closely related to *S.* (*B.*) *stenomphalus* (Pavlov, 1889), if not conspecific. Sazonova (1971, p. 72) mentions that *S.* (*B.*) *mesezhnikowi* is a subjective synonym of *Pavlovites krestnensis* Aristov (*in* Ivanov and Aristov 1969) which, however, appears to remain strongly ribbed.

?*Neotollia* sp.

Plate 5, fig. 3

Material. Two fragments from level D-174, Leira Member of Nybrua Formation.

Remarks. The figured specimen shows the inner crushed whorls; it is involute and bears sharp ribs, which bifurcate close to the middle of the sides. After branching the ribs bend backwards, and ventrally they have a distinct forward projection as they cross the venter.

The specimens may be related to *Neotollia* Shulgina, 1969. The inner whorls of *Neotollia* differ from the closely related genus *Tollia* in having bifurcate and not trifurcate ribs. However, the ribs are sharper and more distant than usually seen in *Neotollia* and also more flexuous on the lateral sides (compare, for example, with the

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EXPLANATION OF PLATE 5

Fig. 1. *Surites* (*Bojarkia*) cf. *mesezhnikowi* (Shulgina). Cast of external mould preserved in sample with *Buchia volgensis*. Dragneset Formation, Ratjønna Member, level D-164, × 1.

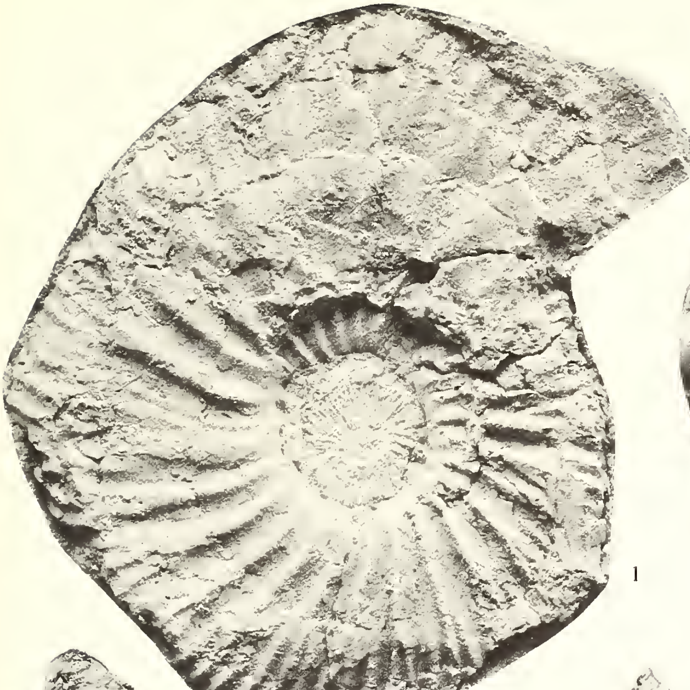
Fig. 2. ?*Lytoceras* sp. Skarstein Formation, Nordelva Member, level E-3, × 1.

Fig. 3. ?*Neotollia* sp. Internal cast. Nybrua Formation, Leira Member, level D-174, × 1.

Figs. 4–6. *Buchia volgensis* (Lahusen). Dragneset Formation, Ratjønna Member, level D-164, × 1. 4, right valve. 5, 6, right valve in anterior and lateral view.

Figs. 7–12. *Buchia keyserlingi* (Lahusen) *s.l.* Nybrua Formation, Leira Member, level D-174. 7, right valve, × 1. 8, left valve, × 2. 9, 10, left valve and posterior view, × 1. 11, 12, left valve and anterior view, × 2.

PLATE 5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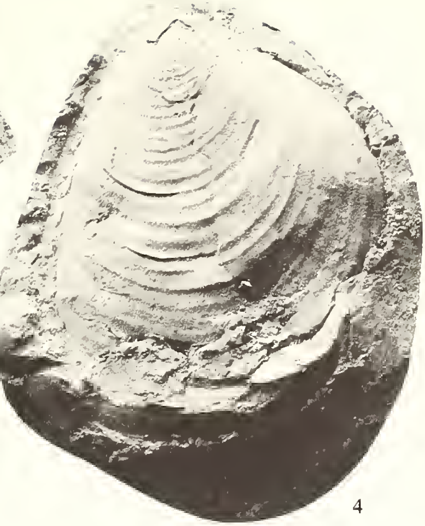
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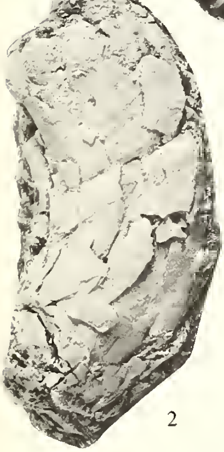
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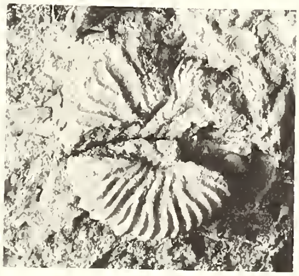
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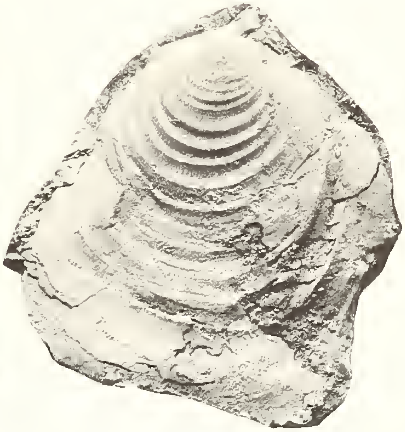
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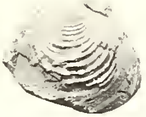
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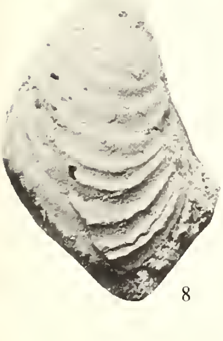
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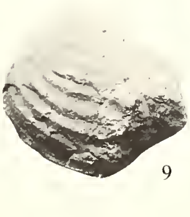
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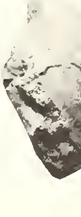
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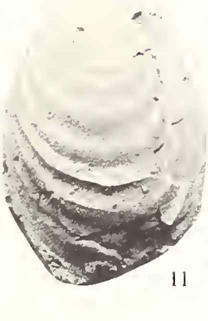
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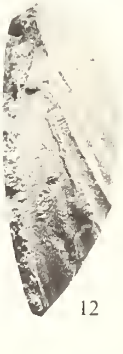
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BIRKELUND, THUSU and VIGRAN, ammonites and bivalves from Norway inner whorls of *N. klimovskiensis* (Krimholz), figured *in* Saks 1972, pl. 5, fig. 5*a*, *b*; pl. 18, fig. 3*a*, *b*). A flexuous pattern may be seen in *Tollia* (for example, *Tollia* cf. *payeri* (Toula) figured *in* Saks 1972, pl. 37, fig. 5).

?*Thorsteinssonoceras* sp.

Material. One poorly preserved specimen from level E-10, Leira Member of Nybrua Formation.

Remarks. The specimen is 16 cm in diameter and wholly septate. It has a polyptychid shape and a completely smooth outer whorl, and may be referred to the genus *Thorsteinssonoceras* Jeletzky, 1965 and not to *Polyptychites* because it grows smooth, but the suture line is not sufficiently well preserved to make a final determination possible.

?*Lytoceras* sp.

Plate 5, fig. 2

Material. One fragment from level E-3, Nordelva Member of Skarstein Formation.

Remarks. The specimen shows a sculpture comparable to *Lytoceras*, but is too poor for closer identification.

Genus BUCHIA Rouillier, 1845

Buchia volgensis (Lahusen, 1888)

Plate 4, figs. 1–4; Plate 5, figs. 4–6

1888 *Aucella volgensis* Lahusen, p. 38, pl. 3, figs. 1–16.
1912 *Aucella volgensis* Lahusen; Sokolov, p. 9, pl. 1, fig. 2.
1959 *Aucella volgensis* Lahusen; Imlay, p. 160, pl. 18, figs. 7, 8, 12–14.

EXPLANATION OF PLATE 6

Selected taxa from Assemblage 1, Middle Jurassic, Andøya, all except figs. 10, 11 from the Ramså Formation, Hestberget Member. All × 1000.

Fig. 1. *Foveotriletes microreticulatus* Couper, 1958. Sample B-27, slide R-27/4, co-ord. 45·0–95·3.

Fig. 2. *Polycingulatisporites triangularis* (Bolkhovitina) Playford and Dettmann, 1965. Sample B-27, slide R-27/1, co-ord. 37·6–95·1.

Fig. 3. *Perotriletes zonatoides* Schulz, 1967. Sample A-59, slide S-59/4, co-ord. 35·3–95·6.

Fig. 4. *Leptolepidites rotundus* Tralau, 1968. Distal sculpture. Sample B-27, slide R-27/2, co-ord. 33·1–96·3.

Fig. 5. *Auritulinasporites scanicus* Nilsson, 1958. Lips thickened, raised as a kyrtome, and emerging into a flange. Sample B-27, slide R-27/2, co-ord. 39·7–99·9.

Fig. 6. *Retitriletes concavus* Schulz, 1966. Distal reticulum with lumina of variable sizes, formed by low and smooth ridges. Sample A-59, slide S-59/2, co-ord. 43·2–106·7.

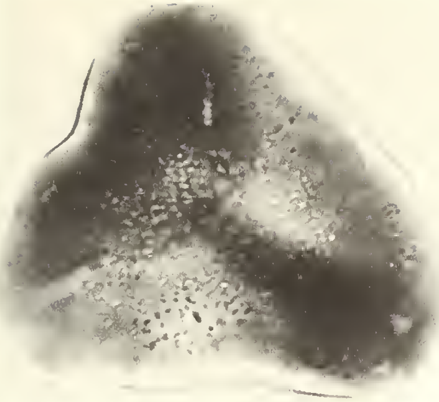
Fig. 7. *Auritulinasporites intrastriatus* Nilsson, 1958. Sample A-59, slide S-59/2, co-ord. 32·0–98·9.

Fig. 8. *Dictyophyllidites mortoni* (De Jersey) Playford and Dettmann, 1965. Proximal focus of well developed kyrtome. Sample A-59, slide S-59/1, co-ord. 43·3–103·3.

Fig. 9. *Chasmatosporites apertus* (Rogalska) Pocock and Jansonius, 1969. Invaginated, supposed sulcoid area. Sample A-37, slide S-37/5, co-ord. 39·2–106·0.

Figs. 10, 11. Spore sp. A. Proximal and distal foci of same specimen. 10, proximal side smooth with exception of three crassitudae parallel to equator. Termination of laesurae widened as auriculae fusing with the cingulum. 11, distal side with muri fusing to an irregular reticulum where the meshes are the size of foveolae. Sample A-69, slide S-69/4, co-ord. 33·8–104·6. Ramså Formation, Kullgrøfta Member.

PLATE 6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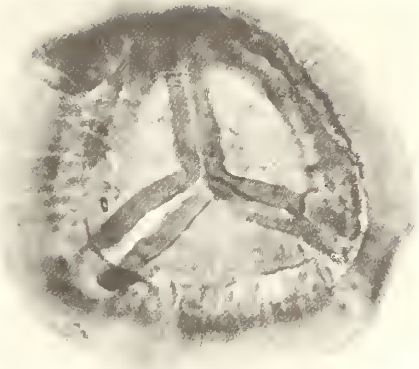
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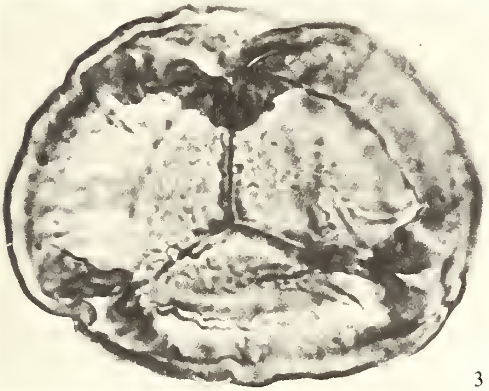
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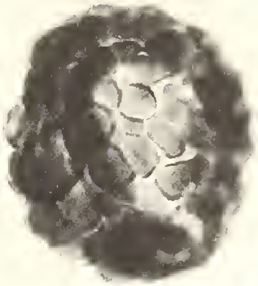
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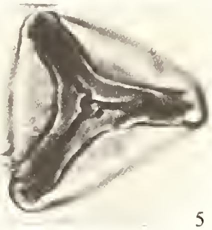
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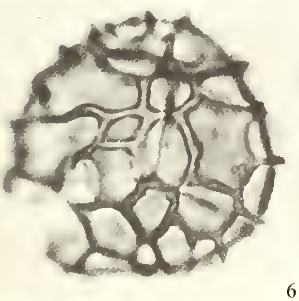
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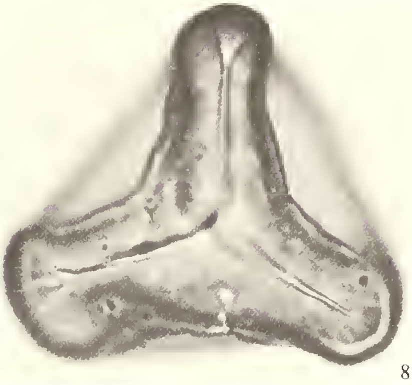
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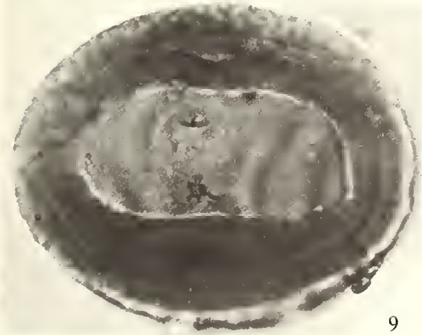
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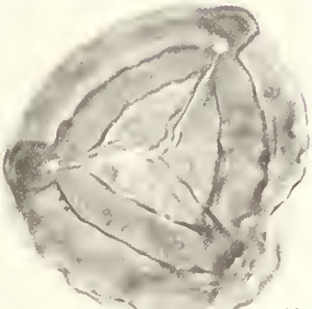
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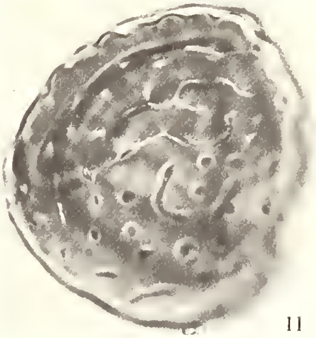
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BIRKELUND, THUSU and VIGRAN, Middle Jurassic spores

Material. A few samples from level D-164 consist largely of *Buchia* shells packed closely together. Most of the shells are fragmentary and crushed. Ratjønna Member of Dragneset Formation.

Remarks. Some of the specimens attain a very large size, as does typical *Buchia volgensis*, but appear to be wider than representatives of that species because of deformation (Pl. 4, fig. 1).

The left valve has a slightly anteriorly curved beak (Pl. 4, fig. 2). The sculpture consists usually of fairly regular, smooth, concentric ribs as in typical representatives of *B. volgensis*, but in a single case weak radial ribs can be distinguished (Pl. 4, fig. 3). The sculpture of that specimen is close to the specimen figured by Pavlov (1896, pl. 27, fig. 2*a–b*) under the name *Aucella volgensis* var. *radiolata* from the Spilsby Sandstone of England.

The right valve (Pl. 5, figs. 4–6) is nearly flat, but again slightly deformed. The ribs are sharper than on the left valve. It shows a well-developed byssal notch.

Buchia keyserlingi (Lahusen, 1888) *s.l.*

Plate 5, figs. 7–12

1888 *Aucella keyserlingi* Lahusen, p. 40, pl. 4, figs. 18–23.
1894 *Aucella keyserlingi* Lahusen; Lundgren, p. 9; text-figs. 1–2.
1912 *Aucella keyserlingi* Lahusen; Sokolov, p. 14.
1965 *Buchia keyserlingi* (Lahusen); Jeletzky, pp. 31, 33, pl. 10, fig. 1; pl. 11, fig. 1; pl. 12, figs. 1, 2; pl. 19, figs. 1, 2, 5, 7.
1969 *Buchia keyserlingi* (Lahusen); Jones, p. A14, pl. 5, figs. 12–15, 18–33.

Material. A sample from level D-174 contains a few fragmentary shells, mostly juveniles. Leira Member of Nybrua Formation.

Remarks. The juvenile specimens are not very diagnostic. Better material is shown by Lundgren (1894, text-figs. 1, 2). The right valve figured on Plate 5, fig. 7 shows the sharp, high, dense ribs characteristic of the species. The specimen shown on Plate 5, figs. 9, 10 seems to be close to *B. keyserlingi* var. *sibirica* (Sokolov 1908, pl. 3, figs. 1–3), which according to Jeletzky (1965, p. 33) is an early form of *B. keyserlingi s.l.*

Acknowledgements. Dr. A. Dalland kindly provided samples and pertinent stratigraphic information, and Dr. J. H. Callomon helped with identification of ammonites and accompanied one of us (T. B.) to British localities. We are grateful to Drs. R. Bromley, R. Casey, R. J. Davey, J. A. Jeletzky, M. K. Howarth, and S. B. Manum for helpful discussion.

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A REVIEW OF THE TRILOBITE FAMILY AULACOPLEURIDAE

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ABSTRACT. The Aulacopleuridae and Otarionidae are considered to be synonymous. The composition and phylogeny of the family are discussed, and new family, subfamily, and generic diagnoses given.

OPINIONS concerning the classification of the trilobite families Aulacopleuridae and Otarionidae have varied; the former was commonly classified with the olenids because of the olenid-like gross morphology of *Aulacopleura*, but both are now universally assigned to the Proetacea. Some authors (e.g. Přibyl 1947, p. 537; Prantl and Přibyl 1951, p. 441) considered the two groups to be subfamilies of the Otarionidae, while Richter, Richter, and Struve (*in* Moore 1959, pp. O382, O403, and O406) regarded them as independent proetacean families. Most subsequent authors have followed the latter classification, though Bergström (1973, p. 42) and Fortey and Owens (1975, p. 230) reverted to that of Prantl and Přibyl, but used Angelin's (1854) name Aulacopleuridae since this has precedence over Otarionidae Richter and Richter, 1926.

The most recent review of the family was that of Prantl and Přibyl (1951). Much information has become available since that date and this paper summarizes our current knowledge of the family.

SYSTEMATIC PALAEONTOLOGY

Order PROETIDA Fortey and Owens, 1975

Family AULACOPLEURIDAE Angelin, 1854

(= Otarionidae Richter and Richter, 1926; Pseudotrinodidae Kobayashi and Hamada, 1972)

Diagnosis. Glabella tapering forwards or subparallel sided, commonly inflated; up to three pairs of glabellar furrows, S1 typically deep and partially defining isolated L1; S2 and S3 weak, shallow, or absent; occipital ring without lateral lobes; preglabellar field usually developed, typically convex; no panderian notch on doublure of free cheek; connective sutures converging backwards, rostral plate usually small and triangular, but may occupy most of doublure or be shaped like an inverted T; thorax of 6–22 segments, no preannulus; pygidium with 2–13 axial rings; pleural areas with 1–7 pairs of ribs with scalloped profile or with posterior pleural band elevated above anterior; cephalic doublure narrow and convex, forming with border a tube; dorsal exoskeleton smooth or granulose.

Stratigraphical range. Ordovician (Tremadoc) to Carboniferous (Dinantian).

Remarks. Most aulacopleurines, and all scharyiines in which the ventral morphology is known, have a small, triangular rostral plate (e.g. Whittington and Campbell 1967,

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pl. 7, fig. 6). In *Harpidella* (*Rhinotarion*) the rostral plate extends forwards beneath the anterior cephalic spine and consequently is shaped like an inverted T (Whittington and Campbell 1967, pl. 4, figs. 10–12). There are no published illustrations of the *Namuropyge* rostral plate, but unpublished work by R.M.O. shows it to be greatly expanded like that of *Brachymetopus* (Owens and Thomas 1975, p. 818) and to occupy almost the whole cephalic doublure. In aulacopleurids and some other Proetacea the cephalic border and doublure form a 'tube' (Fortey and Owens 1975, p. 236; Owens and Thomas 1975, p. 819, text-fig. 2), where the inner margin of the doublure coincides with the border furrow. This doublure structure and type of rostral plate, together with the type of pygidial pleural rib structure, are important in distinguishing aulacopleurids from the superficially similar brachymetopids.

Following Whittington (1960, p. 407) and Owens and Thomas (1975, p. 812) we consider *Tschernyshewiella* Toll, 1899 to be a brachymetopid rather than an otarionid (i.e. aulacopleurid) as believed by Richter, Richter, and Schmidt (*in* Moore 1959, p. O406). The latter authors (p. O407) questionably assigned *Aulacopleurina* Přibyl, 1949 to the family. This genus displays no features by which it could be unequivocally assigned to the Aulacopleuridae, and the deep S2 and S3 furrows and large, well-segmented pygidium (see Schmidt 1958, pl. 1) suggest that it might be more closely related to *Eodrevermannia* (see Moore 1959, fig. 298.8, p. O391). Both genera, however, possibly have origins in the Scharyiinae.

Herein we recognize two aulacopleurid subfamilies—Aulacopleurinae and Scharyiinae. Richter, Richter, and Schmidt (*in* Moore 1959, p. O406) followed Přibyl (1947, p. 538) and Prantl and Přibyl (1951, pp. 441, 475) in assigning *Cyphaspides* to the monotypic subfamily Cyphaspidinae. Although *Cyphaspides* displays some unusual features it is not dissimilar from *Namuropyge* (see discussion p. 78). Because of this, and until the relationships of *Cyphaspides* are clarified, we assign it to the Aulacopleurinae along with *Namuropyge*. We consider the Aulacopleurinae and Otarioninae to be synonymous, and reasons for this are given below.

Subfamily AULACOPLEURINAE Angelin, 1854
(= Otarioninae Richter and Richter, 1926; Cyphaspidinae Přibyl, 1947)

Diagnosis. Glabella commonly strongly inflated; rostral plate small and triangular, or shaped like an inverted T, or occupying most of cephalic doublure; median thoracic axial spine present in several genera, arising from fifth, sixth, or seventh segments; pygidial pleural ribs of scalloped profile, or with posterior pleural band elevated above anterior. Cephalic and pygidial margins entire or spinose.

Genera and subgenera. *Otarion* (*Otarion*) Zenker, 1833; *O*. (*Aulacopleura*) Hawle and Corda, 1847; *Cyphaspides* Novák, 1890; *Cyphaspis* Burmeister, 1843; *Harpidella* (*Harpidella*) M'Coy, 1849; *H*. (*Rhinotarion*) Whittington and Campbell, 1967; *Namuropyge* Richter and Richter, 1939; *Otarionella* Weyer, 1965; *Otarionides* Alberti, 1969; *Pseudotrinodus* Kobayashi and Hamada, 1971*a*.

Genus OTARION Zenker, 1833

Type species. *Otarion diffractum* Zenker, 1833; from Silurian (Ludlow Series), Dlouhá hora, near Beroun, Prague district, Czechoslovakia; by monotypy.

Diagnosis. Aulacopleurine with deep S1 defining isolated, elongate L1; eye small, placed anterior of outer end of S1; preglabellar field convex; rostral plate small and triangular; thorax of 13–22 segments, inner edge of articulating facet about two-thirds of way out from axial furrow; pygidium with 5–8 axial rings and pleural areas much broader anteriorly than axis, with 3–7 pairs of pleural ribs with scalloped profile.

Remarks. The type species of *Aulacopleura* (*A. koninckii*) and *O. diffractum* have many common features. They differ principally in that *A. koninckii* has a more depressed exoskeleton, more thoracic segments with wider pleural areas and no thoracic axial spine, and a proportionately shorter, wider, pygidium (compare Pl. 7, figs. 10 and 3, 5, 6). The two species are evidently closely related and we see no reason to separate them above the subgeneric level.

Subgenus OTARION (OTARION) Zenker, 1833

Type species. As for genus.

Diagnosis. Otarion with faint eye ridge; 13–15 (?17) thoracic segments, axial spine on the sixth.

Stratigraphical range. Silurian (Ludlow Series).

Remarks. The name *Otarion* has been indiscriminately applied to a large number of proetaceans, ranging in age from lower Ordovician to Devonian, because they share a broadly similar morphology. By analysis of character combinations it is possible to restrict *Otarion* as suggested below, and to place many other species in *Cyphaspis* and *Harpidella*. New taxa will eventually be required for other species which cannot at present be placed in any of the above. A full revision of these species is needed since existing descriptions and illustrations are mostly inadequate, cranidia often being the only parts illustrated. As Schrank (1972, p. 25) has indicated, thoracic features are likely to prove useful in defining aulacopleurid genera. The thoracic segments of *Otarion* (*Otarion*) and *O.* (*Aulacopleura*), for example, differ from those of *Cyphaspis* and *Harpidella*; in the former the inner edge of the articulating facet is about two-thirds of the pleural width out from the axial furrow, while in the latter it is about halfway out (Pl. 7, figs. 4*a*, 6, 9, 10). There is also a marked boss on the anterior pleural band at the inner end of the articulating facet in *Cyphaspis* (Pl. 7, fig. 4*b*) and in many *Harpidella* species. Pygidial morphology is also distinctive: *Otarion* (*Otarion*) and *O.* (*Aulacopleura*) have narrow axes and very broad pleural areas, while in *Cyphaspis* and *Harpidella* the axis is as broad as the pleural area (compare Pl. 7, figs. 3, 4*b*). Topotype material of *O. diffractum* is figured here (Pl. 7, figs. 1–3, 5, 6) and this shows the following important features: palpebral lobe small, placed about one-third of the way along the cephalon from the posterior margin; faint eye ridge visible only on internal moulds with a series of further faint ridges behind it (Pl. 7, fig. 2*a*); glabella about as long as wide, subparallel sided; L1 suboval, elongated exsagittally; S1 directed adaxially backwards at first, then parallel to the sagittal line; no distinct S2; anterior border narrow, barely widened sagittally; preocular facial sutures weakly divergent; thorax of 13–15 segments (up to 17 if *O. halli* (Barrande, 1852) is synonymous as Prantl and Přibyl (1951, p. 453) suggest); axial spine on sixth thoracic segment; pygidium with 5–8 axial rings, distinct narrow pygidial border. We consider that the nominate subgenus of *Otarion* should be reserved for forms which closely resemble the type species in these respects. One such is *O. latum* Alberti, 1967 (see Alberti 1969, pl. 34, figs. 5, 6). Other species placed by Alberti in *O.* (*Otarion*) differ in the form of the glabella and length of the preglabellar field.

The type species of *Malayaproetus*, *M. bulbus* Kobayashi and Hamada, 1971*b*, has a long convex preglabellar field, an isolated L1, no occipital lobe, and the poorly segmented pygidium is much wider than long. All these features suggest that the species is an aulacopleurid rather than a proetid. *M. bulbus* is not well known but the general morphology (see Kobayashi and Hamada 1971*b*, pl. 23, figs. 4–6, 8–11) is not unlike that of *O.* (*Otarion*) species, and we tentatively place *Malayaproetus* in the synonymy of that subgenus.

Subgenus OTARION (AULACOPLEURA) Hawle and Corda, 1847

Type species. *Arethusa koninckii* Barrande, 1846; from Silurian (Wenlock Series), Reporyje, Ohrada, Prague district, Czechoslovakia; by monotypy.

Diagnosis. *Otarion* with prominent eye ridge; 18–22 thoracic segments, no axial spine.

Stratigraphical range. Ordovician (Tremadoc Series) to middle Devonian.

Remarks. Chaubet (1937, p. 196) erected the subgenus *Paraaulacopleura*, type species *P. roquemaillerensis* Chaubet, 1937 from the Wenlock of the Montagne Noire, southern France. There are no features by which this species can be separated at the subgeneric level from *A. koninckii* (compare Pl. 7, figs. 9 and 10), and *Paraaulacopleura* is therefore a subjective junior synonym of *Aulacopleura*. In Moore (1959), the type species of *Paraaulacopleura* is not illustrated, the figure given (fig. 309.6, p. O405) being of *A. beyrichi*. This species differs considerably from *roquemaillerensis* in having rather large palpebral lobes and a short preglabellar field—features more typical of

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EXPLANATION OF PLATE 7

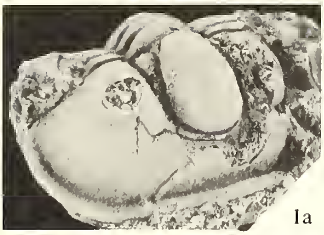
Figs. 1–3, 5, 6. *Otarion* (*Otarion*) *diffractum* Zenker, 1833. Kopanina Formation (Ludlow Series), Dlouhá hora, near Beroun, Czechoslovakia, 1*a*–*b*, BM It 14144, complete, enrolled, partly exfoliated specimen, oblique antero-lateral and lateral views, ×3. 2*a*–*b*, BM It 14149, complete, partly enrolled specimen, palpebral and anterior views, ×3. 3, BM It 14148, partly exfoliated pygidium, dorsal view, ×5. 5, BM It 14143, incomplete thorax and downwardly flexed cephalon, dorsal view, ×4. 6, SM A49357, complete specimen (cephalon flexed downwards), dorsal view, ×3.

Figs. 4, 8. *Cyphaspis ceratophthalma* (Goldfuss, 1843). Devonian (Eifelian), Gees, near Gerolstein, Eifel district, BDR. 4*a*–*b*, NMW 72.47G.4, complete specimen, dorsal view, ×3, and enlarged dorsal view of pygidium and part of thorax, ×5. 8*a*–*b*, NMW 72.47G.3, complete specimen, oblique antero-lateral and lateral views, ×3.

Fig. 7*a*–*b*. *Harpidella* (*Harpidella*) *novella* (Barrande, 1852). Silurian (exact horizon unknown), Lochkov, Czechoslovakia. BM It 14146, cranidium, antero-lateral and dorsal views, ×8.

Fig. 9. *Otarion* (*Aulacopleura*) *roquemailerensis* Chaubet, 1937. Wenlock Series, Roquemaillère, Montagne Noire, southern France. University of Montpelier collection, unnumbered, complete specimen, dorsal view, ×2. Original of Chaubet 1937, plate 6, fig. 1.

Fig. 10. *Otarion* (*Aulacopleura*) *koninckii* (Barrande, 1846). Silurian (probably Litěn Formation, late Wenlock), Loděnice, Czechoslovakia. SM A49395, complete, partly exfoliated specimen, dorsal view, ×3.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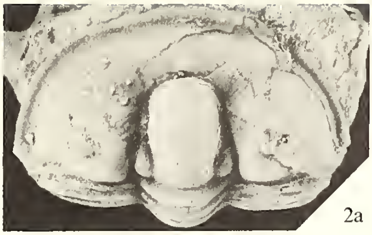
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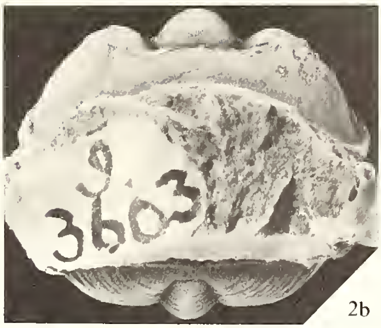

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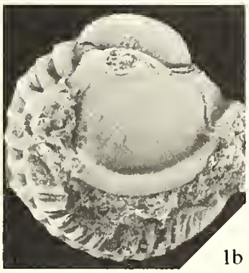
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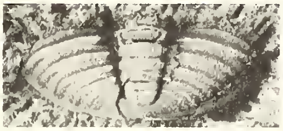
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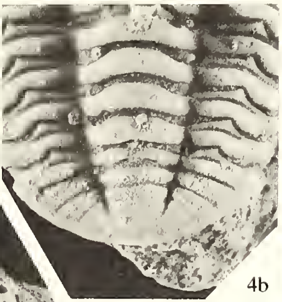
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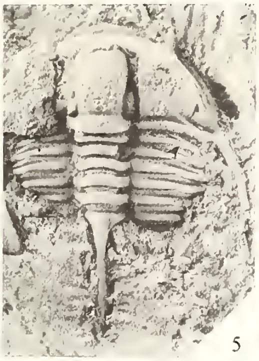
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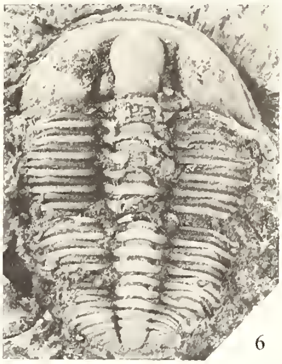
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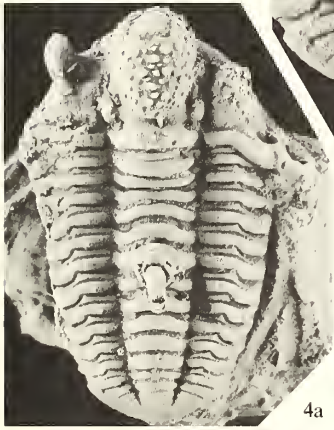
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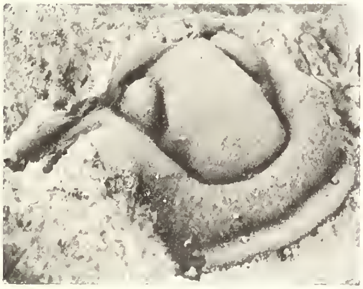
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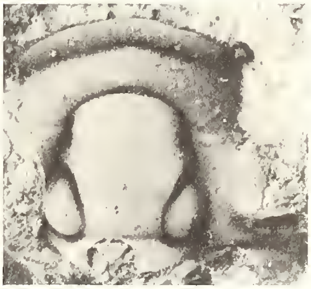
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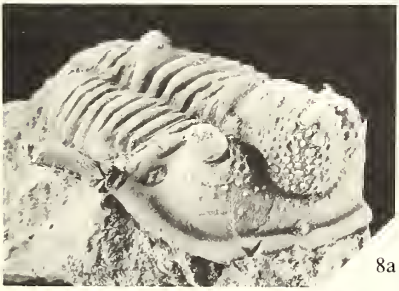
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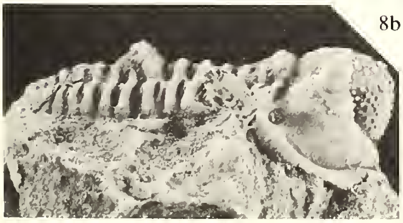
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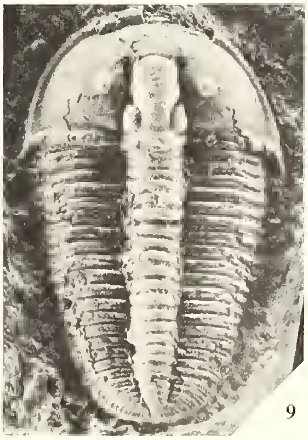
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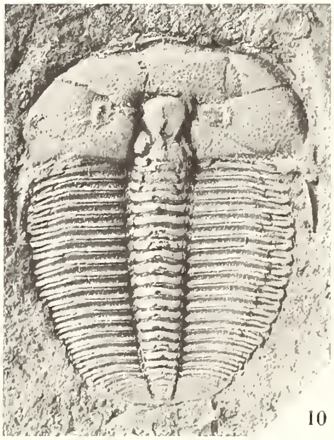
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THOMAS and OWENS, Aulacopleurid trilobites

Harpidella. Most authors appear to have interpreted *Paraaulacopleura* in terms of *beyrichi* rather than *roquemaillerensis*. Species presently assigned to *Paraaulacopleura* can be accommodated in *Aulacopleura* (e.g. *A. ignorata* Alberti, 1969, pl. 36, figs. 14–16), or in *Harpidella* s.l.

Species of *O.* (*Aulacopleura*) are widespread in the Silurian and Devonian but rare in the Ordovician. *Aulacopleura*? *sola* Reed, 1935 (p. 43, pl. 1, fig. 16), from the Caradoc of the Girvan area, does not belong to *O.* (*Aulacopleura*) and may be a dimeropygid. *A. reedi* (see Přibyl 1947, p. 541; Reed 1904, p. 83, pl. 11, figs. 14–15), also from the Caradoc of Girvan, is correctly assigned. The oldest known species of *O.* (*Aulacopleura*) are those described from the Tremadoc and Arenig of China by Lu (1975, pp. 392–395, pl. 34, figs. 8–12).

Genus CYPHASPIDES Novák, 1890

Type species. *Cyphaspides scuticauda* Novák, 1890; from middle Devonian, Greifenstein, German Federal Republic; by subsequent designation of Vogdes 1925.

Diagnosis. Aulacopleurine with forward-expanding clavate glabella, L1 small and inconspicuous; thorax of 11–12 segments, no thoracic axial spine; pygidium with posterior pleural bands elevated above anterior; cephalic and pygidial margins crenulate.

Stratigraphical range. Lower to middle Devonian.

Remarks. The glabellar shape, small L1, and pygidial pleural rib structure make this genus distinct from all other aulacopleurids, although a similar type of rib structure is seen in *Namuropyge* (see below).

Genus CYPHASPIS Burmeister, 1843

Type species. *Phacops ceratophthalmus* Goldfuss, 1843; from Devonian (Eifelian), Gees, near Gerolstein, Eifel district, German Federal Republic; by subsequent designation of Burmeister 1846.

Diagnosis. Aulacopleurine with strongly inflated glabella which projects over short (sag.) preglabellar field in dorsal view; thorax of eleven segments with axial spine on the sixth, prominent 'boss' on anterior pleural band at inner edge of articulating facet, which is about half-way along pleura; pygidial axis short and wide, anteriorly as wide as pleural areas; interpleural furrows only very weakly developed.

Stratigraphical range. Lower to middle Devonian.

Remarks. Following Richter and Richter (1926), most authors have considered *Cyphaspis* to be a junior subjective synonym of *Otarion*. The Richters attributed *Cyphaspis* to Barrande, 1846 and rightly indicated that *C. burmeisteri* Barrande, 1846 is synonymous with *O. diffractum*. *Cyphaspis* was, however, proposed by Burmeister (1843, p. 103) for specimens he considered conspecific with *Calymene clavifrons* Dalman, 1827. Burmeister's specimens are conspecific with those described as *Phacops ceratophthalmus* by Goldfuss (1843). In 1846 (pp. 98–99) Burmeister corrected his mistake and listed *C. ceratophthalma* as the type species of *Cyphaspis*. Prantl and Přibyl (1951, pp. 444–445) discussed the nomenclatural confusion surrounding *Cyphaspis*. They considered *C. ceratophthalma* and *O.* (*O.*) *diffractum* to be congeneric and therefore listed *Cyphaspis* as a synonym of *Otarion*. We have examined topotype material of *C. ceratophthalma* (see Pl. 7, figs. 4*a–b*, 8*a–b*) and this differs from *O.* (*O.*) *diffractum* in its shorter preglabellar field, greater glabellar convexity, stalked eye, deep sulcus at the base of the genal spine, thorax of eleven segments, and thoracic and pygidial characters listed in the remarks under *O.* (*Otarion*) (p. 67). We consider that these differences, which are shared by several species, suffice to separate *Cyphaspis* from *Otarion* at generic level. There are several species which are like the type and closely related species of *Cyphaspis*, but which differ in various details; these range from the late Ordovician to the Devonian, and may require new genera or subgenera. Until they are better known, we refer them to '*Cyphaspis* s.l.'

Genus HARPIDELLA M'Coy, 1849

Type species. Harpes? *megalops* M'Coy, 1846; Silurian (upper Llandovery), Boocaun, Cong, Co. Galway, Ireland; by monotypy.

Diagnosis. Aulacopleurine with rather weakly inflated glabella, wider posteriorly than long, subparabolic in outline; S2 distinct; eye ridge developed; palpebral lobe large, backwardly placed; thorax of 12 segments, axial spine (when present) developed on the sixth segment, inner edge of articulating facet half-way along pleura; pygidial axis weakly defined, as wide anteriorly as pleural areas, with 2–4 rings; pleural areas with 1–2 pairs of ribs with scalloped profile.

Remarks. Many authors, such as Salter (1853), Richter, Richter, and Schmidt (*in* Moore 1959), and Whittington and Campbell (1967), considered *Harpidella* to be synonymous with *Otarion.* We agree with Přibyl (1960), who considered the two to be distinct. The type species of *Harpidella* is known only from cranidia. The holotype and topotype specimens have been figured by Whittington and Campbell (1967, pl. 19, figs. 1–14) and other specimens examined by us. These show the following important features: glabella wider (tr.) posteriorly than long, subparabolic in outline; L1 subtriangular, S1 not strongly curved; S2 short, distinct on both internal and external surfaces; palpebral lobe large, extending back from a point opposite the outer end of S1 to a point opposite mid-L1; distinct eye ridge. In both *H. novella* and *O.* (*O.*) *diffractum* a ridge is developed which arises at the adaxial tip of the eye ridge and curves forwards and outwards across the preglabellar field (Pl. 7, figs. 2*a*, 7*a–b*). The significance of this structure is unknown.

Hawle and Corda (1847, p. 80) selected *Proetus elegantulus* Lovén, 1846 as type species of their genus *Goniopleura*—a generic name preoccupied by Westwood *in* Cuvier (1832, p. 149). Because the cranidium of *P. elegantulus* shares many of the features of *H. megalops* (differing principally in that the anterior border is distinctly longer sagittally than exsagittally—see Lovén 1846, pl. 1, fig. 4*a*) this species can be considered to belong to *Harpidella. H. elegantula* has twelve thoracic segments and the pygidial axis is weakly defined and poorly segmented (see Lovén op. cit.). *H. christyi* (see Hall 1879, pl. 32, figs. 5–7) and a *Harpidella* species from the British Wenlock also have a cranidium like that of *H. megalops* and the thorax and pygidium like those of *H. elegantula.* Whittington and Campbell (1967, p. 461) noted several differences between *H. megalops* and *O.* (*O.*) *diffractum* but argued that *Harpidella* should not be used since *H. novella* (Barrande, 1852), while similar in other respects to *H. megalops*, has a small palpebral lobe which is similarly placed to that of *O.* (*O.*) *diffractum*. Topotype material of *H. novella* (Pl. 7, fig. 7*a–b*) shows that while the palpebral lobe is somewhat smaller than that of *megalops*, it is more posteriorly placed than that of *O.* (*O.*) *diffractum*. Since the other cranidial features of *H. novella* are so similar to those of *H. megalops*, we assign it to *Harpidella*.

Alberti, having first used *Harpidella* (1967, p. 500) for a group of species close to *H. elegantula*, later (1969, p. 383) accepted Whittington and Campbell's (1967, p. 461) arguments for regarding *Harpidella* as a junior subjective synonym of *Otarion* and erected a new subgenus, *Maurotarion*, to accommodate the species previously referred to *Harpidella*. His diagnosis (1969, p. 383) shows that *Maurotarion* differs from *O.* (*O.*) *diffractum* in the same ways as *H. megalops*. We therefore regard *Maurotarion* as a junior subjective synonym of *Harpidella*.

Although the type species of *Harpidella* is not well known, enough features are seen to distinguish it from *O.* (*O.*) *diffractum* and to demonstrate affinities with several other aulacopleurid species. We therefore regard *Harpidella* and *Otarion* as distinct genera.

Subgenus HARPIDELLA (HARPIDELLA) M'Coy, 1849

Type species. As for genus.

Diagnosis. *Harpidella* with no median spine on anterior cephalic border; rostral plate triangular.

Stratigraphical range. Ordovician (Ashgill) to lower Devonian.

Remarks. Chatterton (1971, p. 74) stated that the most distinctive feature of his *Tricornotarion* is the presence of prominent single spines (instead of paired ones) on the glabellae of meraspide cranidia, and considered this feature to be of subgeneric importance. We consider that much more information on aulacopleurid ontogeny is necessary to evaluate the significance of this feature. In other respects *T. struzi* (see Chatterton 1971, pl. 18, figs. 1–18, 33, pl. 19, figs. 13–34), the only known species, is very similar to *H.* (*Harpidella*) species and we therefore place it in the synonymy of that subgenus.

Many Ordovician and Devonian aulacopleurids show similarities to *H.* (*Harpidella*) species. New genera or subgenera will eventually be necessary to accommodate these, but until they are better known, we recommend that they be referred to '*Harpidella* s.l.'

Subgenus HARPIDELLA (RHINOTARION) Whittington and Campbell, 1967

Type species. *Rhinotarion sentosum* Whittington and Campbell, 1967; from Silurian (late Wenlock/lower Ludlow), Baker Pond, Maine, U.S.A.; by original designation.

Diagnosis. *Harpidella* with median part of anterior border drawn forward into projection; rostral plate shaped like an inverted T.

Stratigraphical range. As for type species.

Remarks. The anterior projection of this subgenus is unique in the Aulacopleuridae, and its functional significance is unknown. In other respects the cephalon of *H.* (*Rhinotarion*) is exceedingly like those of species of the nominate subgenus

(Whittington and Campbell 1967, pl. 4; pl. 5, figs. 1–4). All the material of the type species is disarticulated and occurs in association with *H.* (*Harpidella*) species. The pygidium is not, therefore, known with certainty but all the pygidia described by Whittington and Campbell (1967, pp. 464–465, pls. 8, 9) are of similar type. Hence the anterior spine and form of the rostral plate appear to be the only distinctive features of *Rhinotarion*—we do not consider these to be of more than subgeneric importance.

Genus NAMUROPYGE Richter and Richter, 1939

Type species. Namuropyge demaneti Richter and Richter, 1939; from Carboniferous (Viséan, CuIII), Bioul, Belgium; by original designation. [Note: Richter and Richter (1939, pp. 3, 8) gave the horizon of this species as basal Namurian. Dr. P. Sartenaer (pers. comm. to R.M.O., 1975) informs us that the horizon is late Viséan.]

Diagnosis. Aulacopleurine with ankylosed facial sutures; two rows of spines on cephalic margin; rostral plate occupying most of doublure; thorax of 6(?) segments, median spine on fifth (?); pygidial axis with 9–13 rings; pleural ribs with posterior pleural band much elevated above anterior; margin spinose.

Stratigraphical range. Carboniferous, Viséan.

Remarks. The aulacopleurids *Namuropyge* and *Coignouina* Reed, 1943 were based on a pygidium and a cephalon respectively, but discovery of a complete specimen has confirmed that they belong to the same genus (Miller 1977). *Coignouina* is thus a junior subjective synonym of *Namuropyge.*

Genus OTARIONELLA Weyer, 1965

Type species. Cyphaspis davidsoni Barrande, 1852; from Devonian (Eifelian), Koněprusy, Prague district, Czechoslovakia; by original designation.

Diagnosis. Cephalon like that of *Cyphaspis*, but with single row of spines on margin, less strongly inflated glabella, eye not stalked, and sulcus at base of genal spine smaller.

Stratigraphical range. Middle Devonian.

Remarks. The type species of this genus has been included in *Coignouina* (= *Namuropyge*) [e.g. Moore (1959, p. O405, fig. 309.1a)] but differs from the latter in having only one row of cephalic spines and functional dorsal facial sutures. Species with spinose cephalic margins and functional facial sutures are currently included in *Otarionella* (e.g. see Alberti 1969), but it is probable that spinosity has developed independently in several lineages. Some species, for instance, *O. magnificum* (see Alberti 1969, pl. 35, fig. 2*a*), have a glabella and preglabellar field similar to those of *Cyphaspis* species while others (e.g. *O. tafilaltense*—see Alberti 1969, pl. 35, figs. 6*a*, 7*a*) are much more similar to *Otarion* (*Otarion*) *diffractum.*

Only the cephalon of *Otarionella* is known. A full evaluation of the genus must await the availability of more complete material.

Genus OTARIONIDES Alberti, 1969

Type species. Otarion (*Otarionides*) *franconicus* Alberti, 1969; from lower Devonian, Oberfranken, Bavaria, German Federal Republic; by original designation.

Diagnosis. Fixed cheek broad, facial suture nearly straight, gently concave adaxially; palpebral lobe absent (?).

Stratigraphical range. As for type species.

Remarks. This genus was founded on two cranidia, one badly preserved, the other incomplete (Alberti 1969, pl. 34, figs. 8, 9). From these, it is difficult to judge whether or not *Otarionides* possessed eyes.

Genus PSEUDOTRINODUS Kobayashi and Hamada, 1971*a*

Type species. Pseudotrinodus aenigma Kobayashi and Hamada, 1971*a*; from Devonian (late lower/early middle), Kroh, Upper Perak, Malaysia; by monotypy.

Diagnosis. Aulacopleurine with dorsal facial suture ankylosed; blind; rostral plate occupying most of cephalic doublure.

Stratigraphical range. As for type species.

Remarks. Kobayashi and Hamada (1971*a*) described disarticulated remains of a blind Devonian trilobite as an 'agnostoid'. Later (1972, p. 13) they proposed the family Pseudotrinodidae to accommodate it, and concluded (p. 14) that 'The Agnostida is the best order for this family'. The best-preserved figured specimen is an internal mould of a cephalon (Kobayashi and Hamada 1971*a*, p. 398, fig. 2). A reconstruction alongside shows dorsal facial sutures. These are not detectable on the photograph though a crack is present on the left-hand side of the cephalon. Their fig. 4 shows three articulated thoracic segments, the possible remains of a fourth, a detached doublure (= rostral plate) and another cephalon. This cephalon was interpreted by Kobayashi and Hamada as a pygidium—which they used in their reconstruction (1972, p. 14, fig. 3). This also shows a 'median suture' on the underside of the cephalon (an interpretation followed by Bergström 1977), but their 1971*a* fig. 4 clearly shows that the 'suture' is a compression crack.

The *Pseudotrinodus* cephalon, while having some resemblance to those of agnostids, also resembles those of certain aulacopleurids—especially species such as *Cyphaspis* (s.l.) *stigmatophthalmus* Richter, 1914, from the Devonian of Sessacker, Germany (see Richter and Richter 1926, pl. 7, figs. 11–15). If the eyes and facial sutures of such a species were to be lost the result would closely resemble *P. aenigma*. Aulacopleurids such as *Namuropyge*, and brachymetopids such as *Brachymetopus*, have developed rostral plates occupying the entire cephalic doublure in association with ankylosis of the dorsal facial sutures, and this has occurred in *Pseudotrinodus*. We therefore regard *Pseudotrinodus* as an aulacopleurid, and consider this association with a contemporaneous family much more likely than association with the agnostids, the known record of which ends with the Ordovician.

Bergström (1973, p. 37) considered *Pseudotrinodus* to be a proetacean, but did not elaborate further; he later (1977, pp. 97, 102) stated it to be a proetid but gave no reasons for doing so. Since *Pseudotrinodus* probably has at least four thoracic segments (see above), Bergström's (1977, p. 102) statement that it has 'only 3' cannot be substantiated.

Subfamily SCHARYIINAE Osmólska, 1957

Diagnosis. Glabella weakly inflated, triangular or trapezoidal; S1 sometimes shallow or effaced; facial suture normal opisthoparian or cedariiform (in *Scharyia* only); rostral plate small and triangular; thorax of 6–9 segments, median thoracic axial spine absent.

Genera. *Scharyia* Přibyl, 1946; *Panarchaeogonus* Öpik, 1937; *Isbergia* Warburg, 1925; *Cyamops* Owens, 1977.

Remarks. Bergström (1977, p. 102) objected to the inclusion of *Scharyia* in the Aulacopleuridae because of its triangular glabella, large eye, small number of thoracic segments, large pygidium, and because it probably enrolled sphaeroidally, unlike the spiral enrolment 'typical' of aulacopleurids. On the basis of these characters he implied that *Scharyia* was a proetid but did not suggest to which genera it might be related, nor did he comment on *Panarchaeogonus*—the aulacopleurid from which *Scharyia* is believed to have been derived (Owens 1974, p. 687; 1977; Thomas and Owens, this paper).

We can refute all of Bergström's objections to *Scharyia* being an aulacopleurid. Several Ordovician aulacopleurids have a triangular glabella and large eyes (e.g. *Panarchaeogonus whittardi*, see Owens 1974, p. 688, text-fig. 2B), and both *Isbergia* and *Cyamops* have a comparatively small number of thoracic segments and a large pygidium. It is not difficult to derive a comparatively larger pygidium and reduce the number of thoracic segments by tagmosis. We do not consider that the differing styles of enrolment (spiral in such genera as *Otarion* and *Harpidella*, and probably sphaeroidal in *Scharyia*) preclude familial relationship. In the undoubtedly monophyletic Homalonotinae, for example, early species display the spiral enrolment typical of calymenaceans. Later homalonotines have a relatively larger pygidium which renders spiral enrolment impracticable, and here enrolment is sphaeroidal.

Panarchaeogonus appears to be the root stock of the Scharyiinae and shows comparatively few differences from its inferred aulacopleurine ancestors. Owens (1974, 1977) suggested that *Panarchaeogonus* gave rise to *Scharyia* on the one hand, and to *Isbergia* and *Cyamops* on the other. Hence the four genera constitute a discrete phyletic unit which we regard as a subfamily—they display a considerable range of morphology, however, which makes subfamily diagnoses difficult to compose.

For further discussion of this subfamily and its constituent genera see Owens (1974, 1977).

Genus SCHARYIA Přibyl, 1946

Type species. *Proetus micropygus* Hawle and Corda, 1847; from Silurian (Ludlow Series), Klodeník, near Beroun, Prague district, Czechoslovakia; by original designation.

Diagnosis. Scharyiine with triangular glabella, with or without shallow lateral furrows; preglabellar field weakly convex in longitudinal profile; facial suture cedariiform; thorax of 6 segments; pygidium with or without border, margin entire or crenulate; axis with 5–9 rings, pleural areas with 4–6 pairs of ribs; small granule on adaxial end of each thoracic and pygidial posterior pleural band.

Genus PANARCHAEOGONUS Öpik, 1937

Type species. Panarchaeogonus parvus Öpik, 1937; from Ordovician (Llandeilo–Caradoc Series), Kukruse Stage, Kohtla-Jarve, Estonia; by original designation.

Diagnosis. Scharyiine with triangular glabella with distinct L1; palpebral lobe large, close to glabella; weak eye ridge present; three sulci commonly present on posterior part of preglabellar field; thorax of 9 segments; pygidium without border; pygidial axis narrow with 5–9 rings; pleural areas broad, with 5–6 pairs of ribs.

Genus ISBERGIA Warburg, 1925

Type species. Isbergia planifrons Warburg, 1925; from Ordovician (Ashgill Series), Kallholn, Siljan district, Sweden; by original designation.

Diagnosis. Scharyiine with strongly vaulted cephalon; glabella trapezoidal with weak, non-incised furrows; preglabellar field and cheeks strongly declined; no genal spine or eye ridge; thorax of 8 segments; pygidial axis with 5–6 poorly defined rings, pleural areas with 5–6 pairs of ribs; dorsal exoskeleton smooth.

Genus CYAMOPS Owens, 1977

Type species. Cyamops stensioei Owens, 1977; from Ordovician (Ashgill Series), Kallholn, Siljan district, Sweden; by original designation.

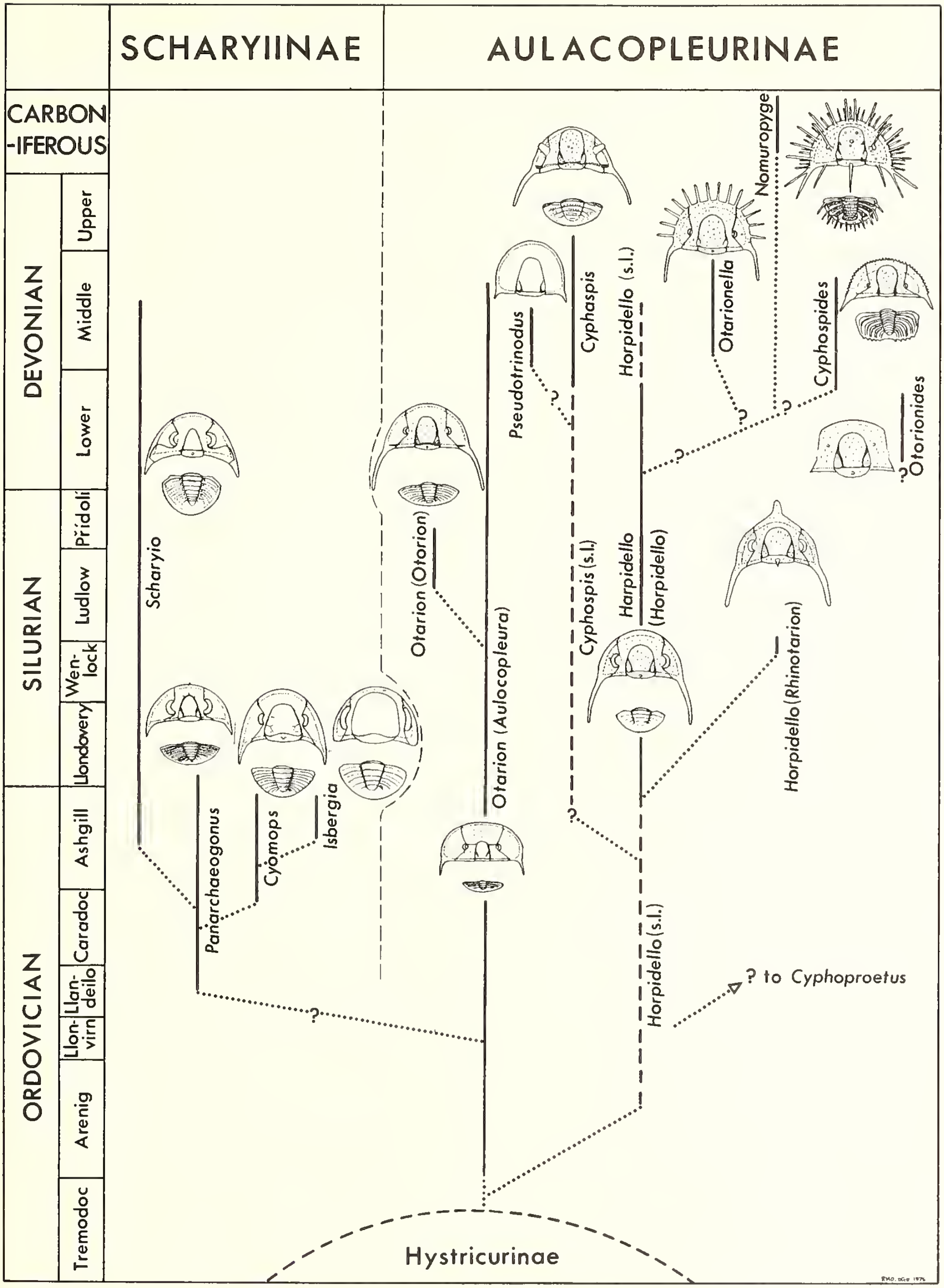
Diagnosis. Scharyiine with trapezoidal glabella, with weakly impressed lateral furrows; preglabellar field sigmoidal or straight in longitudinal section; no eye ridges; thorax of 8 segments; pygidium with conical axis with 6–7 rings; pleural areas broad with 5–6 pairs of ribs, pleural and interpleural furrows reach margin; exoskeleton smooth.

PHYLOGENY OF AULACOPLEURIDAE

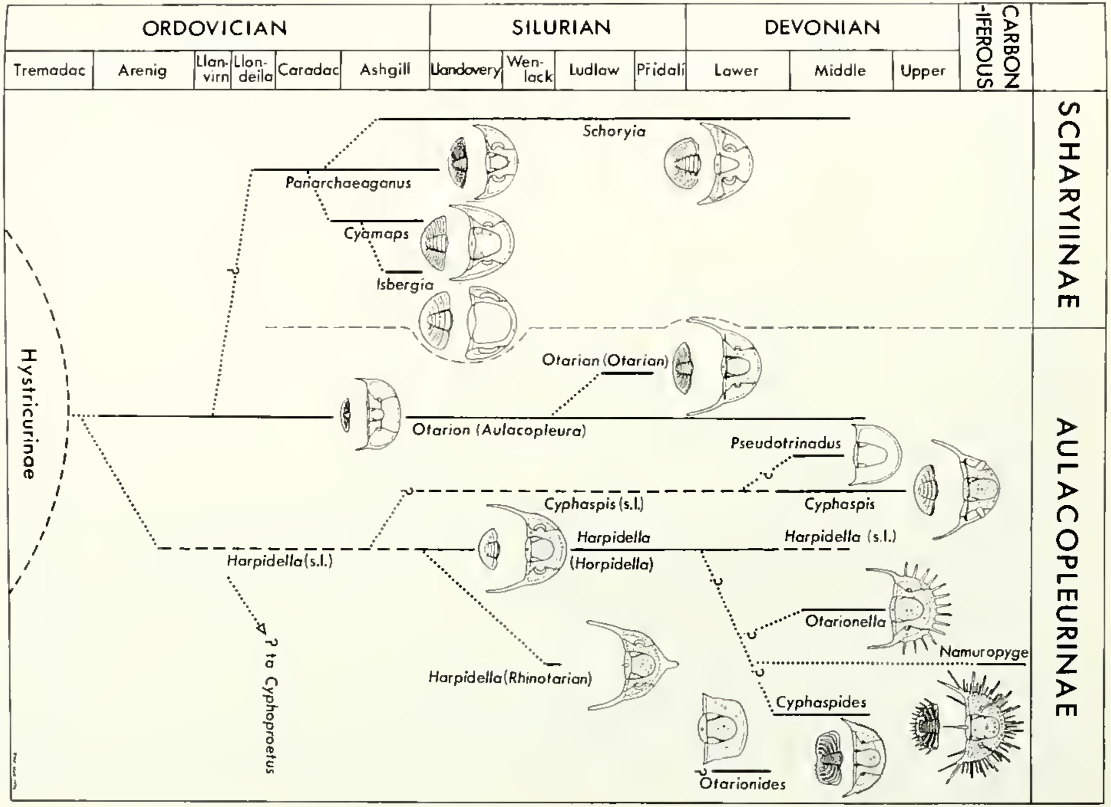
Origins. Aulacopleurids occur only rarely in the early Ordovician and almost certainly evolved in the Tremadoc from hystricurine species (for detailed discussion see Fortey and Owens 1975, pp. 230–231).

Aulacopleurinae. A species of *Otarion* (*Aulacopleura*) occurs in the Tremadoc, the morphology of this subgenus remaining remarkably constant throughout its long range. Fortey and Owens (1975, p. 237) considered that *O.* (*Aulacopleura*) lived in a deep-water environment similar to that previously inhabited by olenids.

Other aulacopleurines occur sporadically in the Ordovician, but their relationships are difficult to determine, principally because most of the material is so fragmentary. A cranidium figured by Whittington (1965, pl. 19, figs. 13, 14, 18) is almost intermediate in morphology between aulacopleurines and *Cyphoproetus* (see Fortey and Owens 1975, p. 229). This suggests that proetines were derived from the Aulacopleurinae in the early Ordovician (see Owens 1973, p. 85). *O. tridens* Ingham, 1970,



TEXT-FIG. 1. Known ranges of aulacopleurid genera, with suggested phylogenetic relationships.



TEXT-FIG. 1. Known ranges of aulacopleurid genera, with suggested phylogenetic relationships.

from the Ashgill of the English Lake District, is in some ways similar to *Harpidella* species (having rather large, posteriorly placed palpebral lobe; moderately divergent preocular facial sutures; subtriangular L1; poorly segmented pygidium). It differs in having pointed pleural tips to the anterior three thoracic segments, an axial spine on the seventh (not sixth) thoracic segment, and only eleven (not twelve) thoracic segments. A species almost intermediate in morphology between '*O.*' *tridens* and *Cyphaspis* species occurs in the British Wenlock indicating that the latter genus and its allies might not have its origins in *O.* (*Otarion*), though cephalic features of the two are closely similar.

Aulacopleurines are remarkably conservative throughout the Ordovician and Silurian, major innovations such as spinosity, eye reduction and blindness, ankylosis of the facial sutures, enlargement of the rostral plate, and changes in the pygidial pleural rib structure, not occurring until the Devonian.

The origins of *Namuropyge* are uncertain. It possibly evolved from *Otarionella* by ankylosis of the dorsal facial sutures and the development of a second row of marginal cephalic spines. Unfortunately, the pygidium of *Otarionella* is unknown, so that comparison with that of *Namuropyge* is not possible. *Namuropyge* pygidia do, however, resemble those of *Cyphaspides* species in rib structure, but the cephala of the two genera are quite different, those of the latter having a clavate glabella and very small, inconspicuous L1. It is possible that *Namuropyge*, *Cyphaspides*, and *Otarionella* have a common origin in *Harpidella* or *Cyphaspis*. *Otarionides* is poorly known but it illustrates a trend common in Devonian Proetacea—outward migration and concomitant reduction, and finally loss, of eyes. The blind *Pseudotrinodus* appears to be an end member of such a line.

Scharyiinae. Owens (1974, 1977) has discussed possible interrelationships between scharyiine genera. These may be summarized as follows: *Panarchaeogonus* appears in Llandeilo-Caradoc times, and probably had its origins in the Aulacopleurinae in the Llandeilo or earlier (its pygidium suggests that its most likely ancestry is in *Otarion* (*Aulacopleura*)). *Cyamops* and *Isbergia* are both characteristic of Ashgill reefs. The former's earliest representative is from the late Caradoc, and it was probably derived from *Panarchaeogonus*. *Cyamops* is similar to *Panarchaeogonus*, differing principally in lacking eye ridges, in glabellar outline, very shallow S1, and in having only eight thoracic segments. *Isbergia* is of unusual aspect for an aulacopleurid (see Fortey and Owens 1975, p. 236), the steeply declined cheeks and preglabellar field giving it an appearance superficially similar to the illaenid *Panderia*. The absence of a pre-annulus and the type of pygidial pleural rib structure, however, clearly indicate that it is an aulacopleurid. Apart from the strongly vaulted cephalon *Isbergia* is similar to scharyiines, especially *Cyamops* (eye position, lack of eye ridge, weak lateral glabellar furrows, eight thoracic segments, no thoracic axial spine, number of pygidial axial rings and pairs of pleural ribs, lack of sculpture) and we regard it as being derived from that genus by modification of the cephalon. The earliest *Scharyia* species are from the Ashgill. Owens (1974, p. 687) suggested that *Scharyia* evolved from *Panarchaeogonus* through release of fewer segments into the thorax during ontogeny, producing a short thorax of six segments and a relatively longer pygidium, and by the acquisition of a cedariiform facial suture.

Repositories. BM—British Museum (Natural History), London; NMW—National Museum of Wales, Cardiff; SM—Sedgwick Museum, Cambridge.

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A PRIMITIVE PARASUCHID (PHYTOSAUR) REPTILE FROM THE UPPER TRIASSIC MALERI FORMATION OF INDIA

by SANKAR CHATTERJEE

ABSTRACT. Two nearly complete and articulated parasuchian (phytosaur) skeletons, recently discovered from the Upper Triassic Maleri Formation of India, allow a detailed osteological description and restoration of the species *Parasuchus hislopi* Lydekker, 1885. The skull shows almost all of the archaic characters of parasuchians listed by Gregory (1962). The well-preserved braincase permits a reconstruction of the brain from a latex-rubber cast of the brain cavity. The tooth-replacement cycle of an individual tooth has been worked out from serial sections of a premaxilla. The parasuchian tarsus, hitherto poorly known, shows the basic crocodilian pattern of ankle joint. The mode of life of this carnivorous reptile is considered.

The extremely close relationship between *Parasuchus* and *Paleorhinus* from the early Upper Triassic of North America, indicates generic identity; the latter becomes a subjective junior synonym of the former. The family group name Parasuchidae Lydekker, 1885 is herein reinstated. *Parasuchus* also permits a more accurate dating of the Maleri Formation; the suggested age ranges from Late Carnian to Early Norian. Possible evolutionary trends within the family are outlined, and phenetic and phylogenetic relationships are suggested.

THE parasuchians (phytosaurs) are long-snouted, carnivorous reptiles of Late Triassic age superficially resembling the modern crocodiles in size, proportions, and inferred activities. However, certain anatomical differences separate these two related groups into two different orders. The parasuchians are most abundantly recorded from Europe, India, and North America. Their remains from North Africa, China, and Madagascar are insufficiently known at present. Rapid structural modifications during a brief geological period, combined with fairly wide geographical distribution, make them potentially very useful for a palaeontological subdivision of the Late Trias.

The Indian parasuchian, *Parasuchus hislopi*, was first described by Lydekker (1885, p. 22, pl. 3) from a number of fragmentary specimens from the Maleri Formation of the Pranhita-Godavari Valley. Lydekker also mentioned the occurrence of a parasuchian from the Tiki Formation of the Son-Mahanadi Valley, without any formal designation. Further surface collections of parasuchian material from the Maleri and Tiki Formations were acquired by the Geological Survey of India from time to time, and the material was reviewed by von Huene (1940) and Colbert (1958).

Gregory (1962), while critically evaluating the parasuchian genera of the world, commented that the available Indian parasuchian material was too incomplete for diagnostic value. This deficiency was remedied by the discovery, during the winter of 1965/1966, of two nearly complete and articulated parasuchian skeletons from the Maleri Formation (Chatterjee 1967). These are the most complete skeletons of parasuchians to be discovered anywhere in the world. In the previous year, a parasuchian skull was found by Mr. T. S. Kutty in the Tiki Formation. Two more skulls of parasuchians were subsequently collected from the Maleri rocks in 1973–1974.

[Palaeontology, Vol. 21, Part 1, 1978, pp. 83–127, pl. 8.]

The new material described below considerably amplifies our knowledge of *Parasuchus* and permits reconsideration of this parasuchian's affinities and its stratigraphic significance. This paper is a projected series of studies of the Gondwana vertebrates of the Pranhita-Godavari Valley by the Geological Studies Unit of the Indian Statistical Institute.

Parasuchus is found in two closely related formations of Gondwana sediments—namely the Maleri Formation of the Pranhita-Godavari Valley, and the Tiki Formation of the Son-Mahanadi Valley; both are Late Triassic in age. In India, Gondwana sediments occur as relatively restricted strips and patches in several river valleys. In the Pranhita-Godavari Valley, these deposits crop out in a narrow elongated basin covering parts of Andhra Pradesh and Maharashtra, extending NNW from near the coast for about 220 miles length with an average width of 25 miles, and following the general trend of the present river valley. The Gondwana sediments within the basin are flanked on either side by Precambrian rocks. The Maleri is a red-bed formation consisting mainly of red clays with subordinate sandstones and lime-pellet rocks. The Triassic sequence in the Pranhita-Godavari Valley is shown in Table 1.

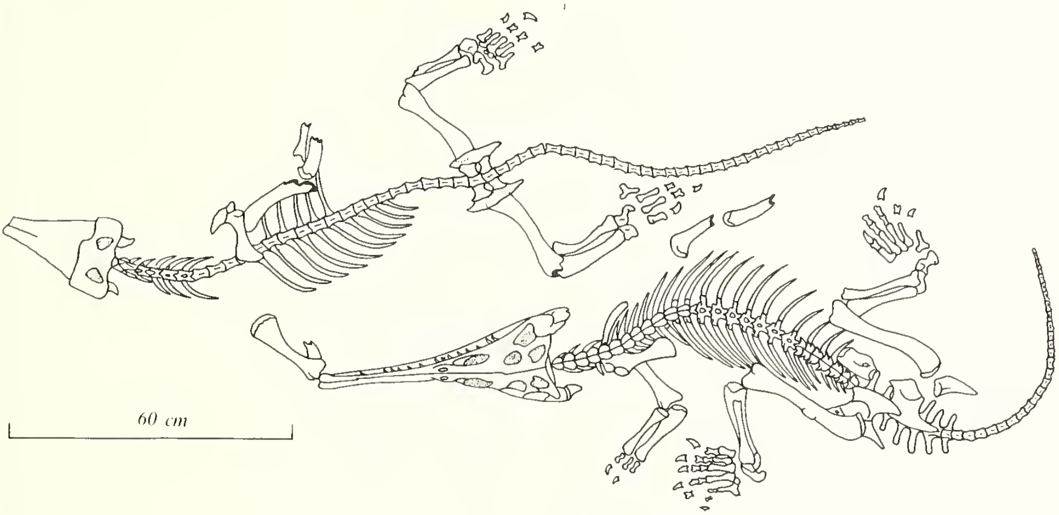
TABLE 1

Formation	Main lithologies	Characteristic fossils	Age
Dharmaram	Sandstones with red clays	Plateosaur, thecodontosaur	Late Upper Trias (Upper Norian and Rhaetian)
Maleri	Sandstones, red clays and lime-pellet rocks	Dipnoi, metoposaur, rhynchosaur, parasuchian, aetosaur, coelurosaur, thecodontosaur, traversodont	Early Upper Trias (Carnian through Early Norian)
Bhimaram Sandstone	Sandstone with intercalated red clays	Fragmentary remains, indeterminate	(?Ladinian)
Yerrapalli	Red clays and sandstones	Capitosaur, ?brachyopid, dicynodonts, erythrosuchid, trirachodont cynodont, rhynchosaur	Middle Triassic (Anisian)

The Tiki Formation, so far, the only representative of the Triassic sequence in the Son-Mahanadi Valley, can be equated with the Maleri Formation by its lithology and fossil content. Good skull material of parasuchians, metoposaurs, and aetosaurs has been discovered recently from the Tiki Formation and will be described soon.

MATERIAL AND METHODS

The new and associated parasuchian material from the Maleri Formation was found in red clay very near to the surface in the vicinity of Mutapuram village (lat. 19° 8′ N., long. 79° 40′ E.) of Adilabad District, Andhra Pradesh. Some fragments were scattered on the surface and a series of associated vertebrae were showing through the clay. After careful removal of the clay, two complete parasuchian skeletons were exposed. Both the animals were roughly 8 ft in length, lying on their ventral surface side by side (text-fig. 1). The right individual, as seen from the rear, lies a little ahead of the left. The skull of the left individual is better preserved; much of the right skull has been washed away. The body shows the general curvature and a life-like pose. Almost all of the bones were found in position, including the scutes. The two skeletons were taken out as they lay, articulated in a single block of clay of 10 × 8 × 1 ft. The block was gradually encased in a crate made of wooden beams and planks screwed and bolted together. Crate and specimen, when finished and lifted, weighed about 2 tons. The bones were cracked in some places but held together by cementation and are otherwise well preserved. The preparation has been done mechanically using pin vice and brush. Acetic acid was occasionally used for removing the calcareous coating of the bone.



TEXT-FIG. 1. *Parasuchus hislopi* Lyd. (× 0·08). Two associated skeletons, as found in Mutapuram village, Dt. Adilabad, A.P., India; *top*, specimens ISI R 43; *bottom*, ISI R 42.

A couple of miles north of this site, two more parasuchian skulls were recovered near the Venkatapur village in an excellently preserved condition. The solitary skull from the Tiki Formation was found in a loose boulder of hard calcareous sandstones, about 4 miles west of Tiki village (lat. 23° 56′ N., long. 81° 22′ E.) of Shadol District, Madhya Pradesh. Except for the snout and the squamosal, the skull is otherwise complete and well preserved. Acid preparation was found ineffective. Small cold chisels and a light hammer were employed for removing the hard matrix. A vibro-tool was safely used very close to the bone as this lent itself to much finer control.

The material used in the following description comprises the following specimens.

Indian Museum Collection, Calcutta. GSI H20/11: the lectotype specimen; part of the premaxillary snout, from Maleri.

Geology Museum, Indian Statistical Institute, Calcutta. ISI R 42: left individual of the articulated parasuchian from the Maleri, as seen from the rear; ISI R 43: right individual of the articulated parasuchian from the Maleri, as seen from the rear; ISI R 44: skull, from Tiki; ISI R 45: isolated basioccipital from Maleri; ISI R 46: isolated conjoined basioccipital/basisphenoid from Maleri; ISI R 47: isolated conjoined basioccipital/basisphenoid from Maleri; ISI R 160: an isolated skull, from Maleri; ISI R 161: part of the skull and postcranial, from Maleri.

SYSTEMATIC PALAEONTOLOGY

Order THECODONTIA
Suborder PARASUCHIA Huxley, 1875
Family PARASUCHIDAE Lydekker, 1885
Subfamily PARASUCHINAE Lydekker, 1885
Genus PARASUCHUS Lydekker, 1885
Parasuchus hislopi Lydekker, 1885

Plate 8; text-figs. 1–15

Type species. Parasuchus hislopi Lydekker, 1885.

1940 *Brachysuchus* (?) *maleriensis*; von Huene, p. 6.
1958 *Phytosaurus maleriensis*; (von Huene) Colbert, p. 75.

Diagnosis. See p. 114.

Lectotype. Premaxillary rostrum, GSI H 20/11, housed in the Indian Museum, Calcutta.

Type locality. Maleri village in the Adilabad district, Andhra Pradesh.

Horizon. Maleri Formation of the Gondwana Group in the Pranhita-Godavari Valley, Late Triassic.

History of classification. The nomenclatural history of *Parasuchus hislopi*, and its supraspecific taxa, has been, until recently, highly confused. Huxley (1870, p. 49) first used the name *Parasuchus* in a faunal list without any diagnosis, and thus his name was a *nomen nudum* until 1885, when Lydekker (p. 22) validated it and proposed a formal family group name Parasuchidae. Unfortunately, the type species of *Parasuchus*, *P. hislopi* Lydekker, 1885, has as syntype material a rhynchosaurian basicranium mixed with parasuchian bones, scutes, and teeth. Von Huene (1940, p. 6) identified the basicranium as belonging to the rhynchosaur *Paradapedon huxleyi* (Lydekker) 1881; thus he attempted to suppress the name *Parasuchus hislopi* and coined a specific name 'aff. *Brachysuchus*' *maleriensis* for the Maleri parasuchian. Later Colbert (1958, p. 75) designated all the Indian parasuchian material as *Phytosaurus maleriensis*. Gregory (1962) thought that the Indian parasuchian material lacked the critical portions for comparisons and was too incomplete for diagnostic value; he provisionally accepted Colbert's proposition.

The new and fairly complete specimens clearly show that the Indian parasuchian is rather primitive and distinctive, and is not generically identical with either *Brachysuchus* Case, 1929 (= *Angistorhinus* Mehl, 1913) or *Phytosaurus* Jaeger, 1828 (= *Nicrosaurus* Fraas, 1886).

Since the rhynchosaur basicranium is neither the holotype of *Parasuchus hislopi*, nor the lectotype of *Paradapedon huxleyi*, the suppression of *Parasuchus hislopi* can be avoided to preserve the stability of nomenclature, and to meet Lydekker's original intention (that is, that the name should apply to a parasuchian). Chatterjee (1974) validated the name *P. hislopi* for the Indian parasuchian after carefully selecting a premaxillary rostrum as the lectotype from the original syntypes of Lydekker.

Once the name *P. hislopi* is established on a sound basis, there is a strong case for using names based on *Parasuchus* for higher categories as they are still available. The name Parasuchia was coined by Huxley (1875, p. 427) as a subordinal taxon for parasuchian genera (including aetosaurs, as then understood). Lydekker (1885, p. 22) first proposed the family group name Parasuchidae based on the nominal genus *Parasuchus*. Later, he (1888) erected a second family Phytosauridae to include *Phytosaurus* Jaeger, 1828. McGregor (1906, p. 91) raised the Parasuchia to ordinal rank, containing two suborders Phytosauria and Aetosauria. He included all the known long-snouted parasuchian genera within a single family Phytosauridae. Later von Huene (1915, p. 492) established a new family Mystriosuchidae to include all the parasuchian genera except *Phytosaurus* which he regarded as the sole member of the Phytosauridae. In a subsequent revision, he (1922) referred Parasuchia as a suborder. Since then the name Parasuchia continued in general use for the suborder (Romer 1956, p. 597; Charig 1967, p. 709). Camp (1930) and Gregory (1962) accepted a single family group name Phytosauridae containing all parasuchian genera.

It appears from this discussion that three family names were proposed for the parasuchian genera from time to time: Parasuchidae Lydekker, 1885, Phytosauridae Lydekker, 1888, and Mystriosuchidae von Huene, 1915. According to code of zoological nomenclature, a family group name formed by the union of two or more taxa of that group takes the oldest valid name (Stoll *et al.* 1964, Article 23 (d) (1)). Thus Parasuchidae Lydekker, 1885 has a clear priority over Phytosauridae Lydekker, 1888, and Mystriosuchidae Huene, 1915. In addition, *Phytosaurus* is now regarded as indeterminable (Gregory and Westphal 1969). It is also a singularly inappropriate name for a carnivore. Parasuchidae Lydekker, 1885 is re-established herein as the sole family group name for all parasuchian genera of a distinctive suborder Parasuchia of the Order Thecodontia.

The Indian genus *Parasuchus* and the North American primitive form *Paleorhinus* are so similar in structure, as discussed in a later section, that it is difficult to differentiate between them at a generic level. *Paleorhinus* Williston, 1904 is considered here as a subjective junior synonym of *Parasuchus* Lydekker, 1885. Recognizing *Parasuchus* and *Paleorhinus* as subgenera seems to be a useful compromise which permits expression of close relationship between two geographically separated populations.

Gregory (1962), on the other hand, suggested that the German form *Francosuchus* Kuhn, 1932 is congeneric with *Paleorhinus* Williston, 1904. However, *Francosuchus* appears to be more divergent phylogenetically than *Paleorhinus* and it would seem logical to regard it as a genus in its own right. There are good arguments in favour of a subfamilial dichotomy, the branches of which may be labelled as Parasuchinae and Mystriosuchinae (see discussion in a later section). The subfamily Parasuchinae (*nom. transl. ex* Parasuchidae Lydekker, 1885) includes *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon*. The subfamily Mystriosuchinae (*nom. transl. ex* Mystriosuchidae von Huene, 1915) includes *Francosuchus* and *Mystriosuchus*.

There is no evidence that the Indian parasuchian material now in the Maleri and

Tiki Collections, represents more than one species. The slight variability encountered may result from differences in sex and age.

Description of Parasuchus hislopi: *Skull.* Specimens ISI R 42, ISI R 44, ISI R 160, and ISI R 161 were used as a basis for the study of the skull. The specimens are undistorted and well preserved. ISI R 42 is fairly complete and is the basis for restoration. ISI R 44 displays the endocranial structure in great detail.

A table of the main measurements in millimetres of *Parasuchus* specimen ISI R 42 is as follows:

TABLE 2

Skull length	585
Skull width	182
Skull height	105
Prenarial length (measured from anterior border of the nares)	305
Postnarial length	280
Distance from rear of naris to front of orbit	110
Interorbital width	30
Preorbital length (measured from anterior border of the orbit)	453
Postorbital length	132
Total length of the mandible	622
Length of the symphysis of the mandible	327
Presacral column length	900
Scapulocoracoid height	195
Breadth apex of scapula	60
Coracoid breadth	110
Clavicle length	117
Interclavicle length	200
Humerus length	182
Humerus, least diameter of the shaft	22
Radius length	122
Radius, least diameter of the shaft	12
Ulna length	135
Ulna, least diameter of the shaft	17
Manus length	120
Ilium, crest length	126
Ilium, breadth of neck	62
Ilium height	105
Ischium height	125
Pubis height	105
Total length of the puboischiadic plate	200
Femur length	240
Femur, least diameter of the shaft	26
Tibia length	153
Tibia, least diameter of the shaft	18
Fibula length	158
Fibula, least diameter of the shaft	14
Pes length including tarsus	212
Estimated total length	2700

Dermal bones of the skull roof (text-figs. 2–4; Pl. 8). The septomaxillae are small forming a bar between the nares. In specimen ISI R 42, the nasals are elevated into narrow rims around the nares, whereas in specimens ISI R 44 and ISI R 161, the nasals are flat. The presence or absence of elevated rims around the nares is regarded by Camp (1930) as a sexual character—according to him, the former is the female, the latter the male.

The lachrymal extends anteriorly as a narrow depressed rim bordering the antorbital fenestra postero-dorsally and receives a similar rim of the maxilla on the opposite side of the fenestra. The supratemporal fenestrae are small, triangular, and lie at the level of the skull roof. The infratemporal fenestrae are fairly large. Inside each of the supratemporal fenestrae, a flange of the parietal turns downwards to meet the

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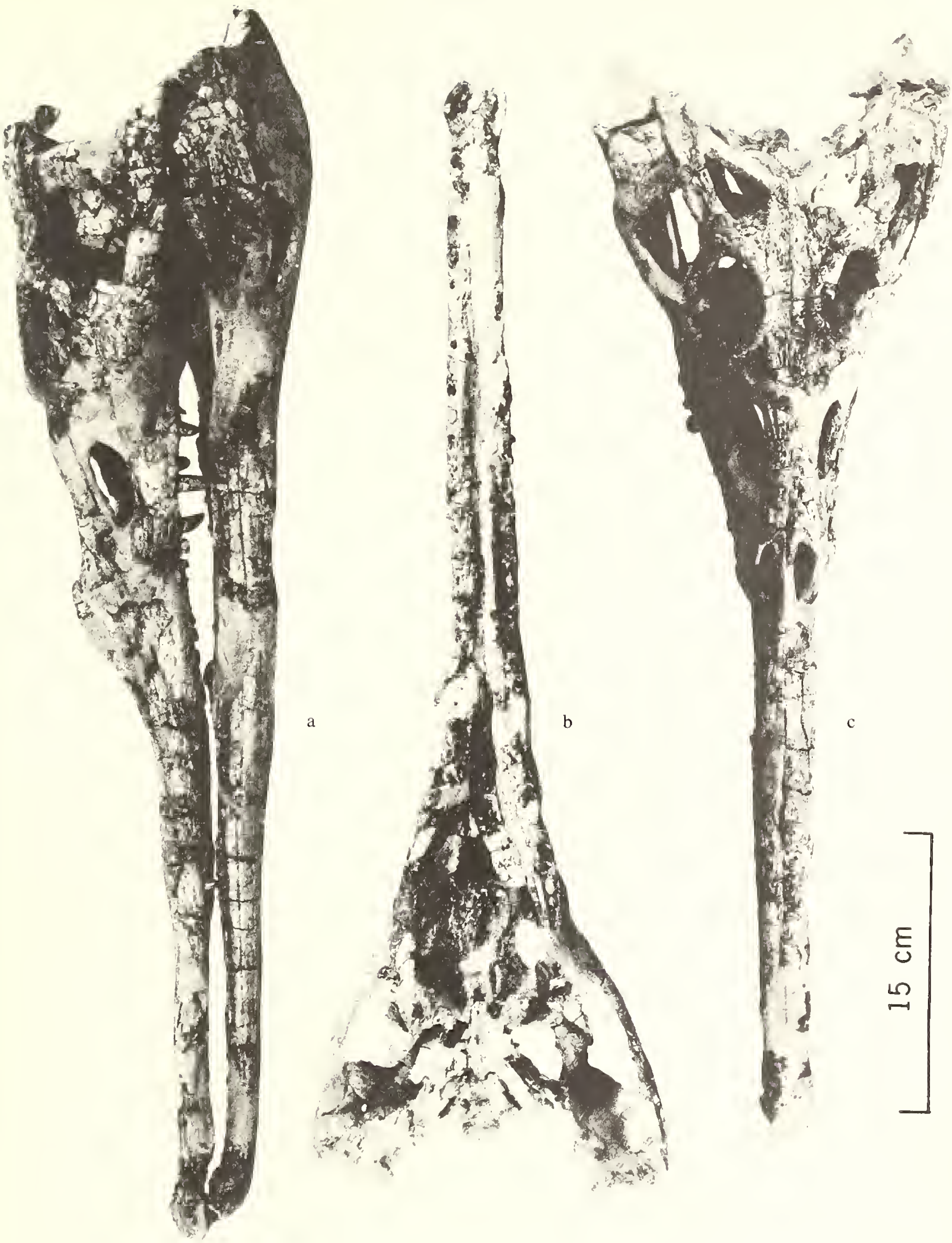
EXPLANATION OF PLATE 8

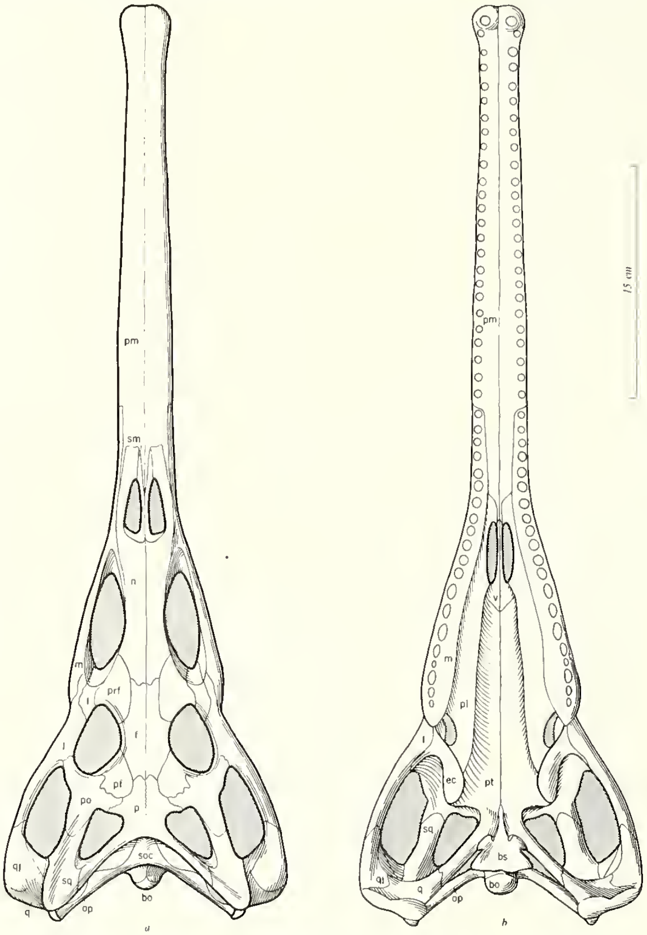
Parasuchus hislopi Lyd. (×0·3). Specimen ISI R 42, Skull. *a*, left lateral view; *b*, ventral view; *c*, dorsal view.



CHATTERJEE, Indian reptile *Parasuchus*

laterosphenoid. Posteriorly each parietal is extended laterally and ventrally as a lens-shaped process that joins the supraoccipital below.

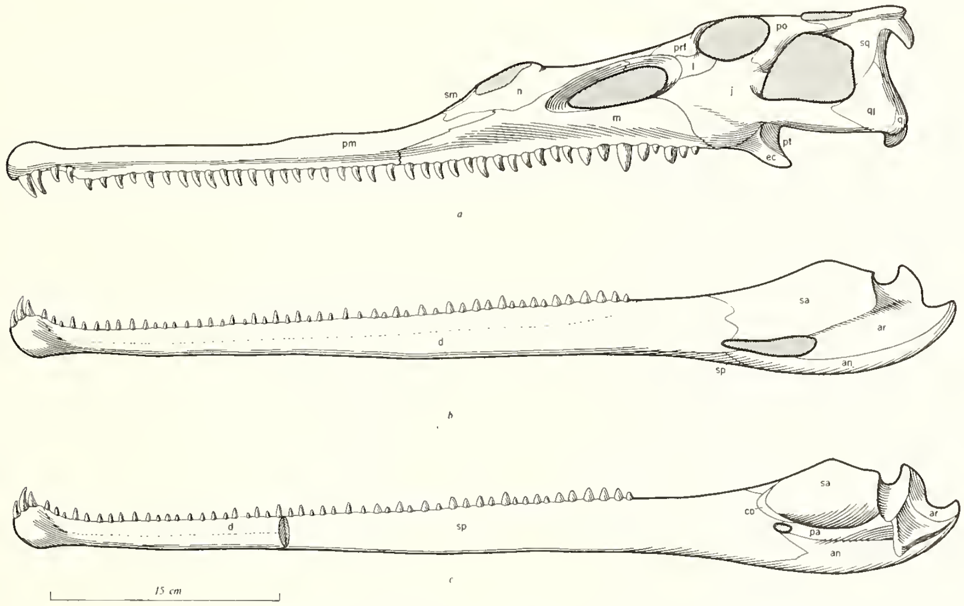
No interparietals have been found. Camp (1930) recognized interparietals and tabulars only in a juvenile skull of *Machaeroprosopus* (= *Rutiodon*); these are probably fused with the supraoccipital and parietals respectively in the adult form.



TEXT-FIG. 2. *Parasuchus hislopi* Lyd. (× 0·20). Restoration of the skull; *a*, dorsal view; *b*, ventral view.

Abbreviations: a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; c, coronoid; cp, crista paroccipitalis; d, dentary; ec, ectopterygoid; ef, epipterygoid foramen; eo, exoccipital; es, endolymphatic sac; euf, eustachian fossa; fo, fenestra ovalis; hf, hypophyseal fenestra; ic, foramen for internal carotid; is, interorbital septum; j, jugal; jf, jugular foramen; l, lachrymal; ls, laterosphenoid; m, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; pra, prearticular; prf, prefrontal; prs, presphenoid; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sf, stapedial fossa; soc, supraoccipital; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal; v, vomer; vc, vestibular cavity. Foramina for cranial nerves in Roman numerals.

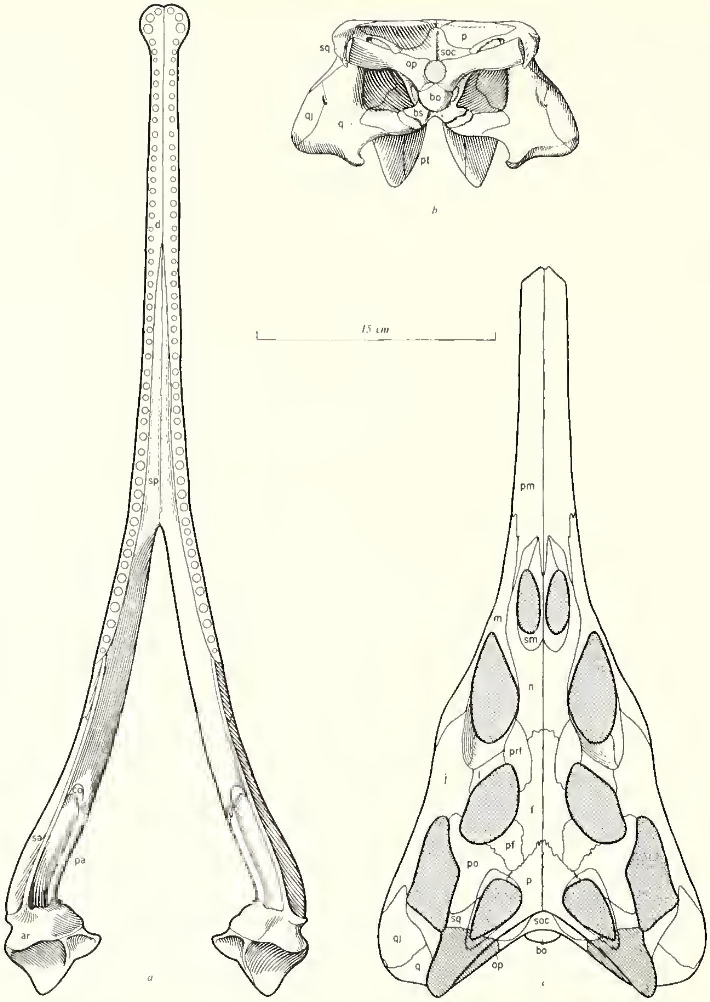
The quadrate is held rigidly by the squamosal dorso-laterally and by the quadratojugal anteriorly. Below the head, it makes a short contact with the paroccipital process. Mesially a deep flange is produced as a pterygoid wing to receive the overlap of the quadrate ramus of the pterygoid. The ventral condylar surface is of uniform width, slants mesially, and shows a double keel for articulation with the lower jaw. The epipterygoid is incompletely known. Dorsally it fits into a pit of the laterosphenoid, while the ventral flattened end sits on the dorsal surface of the pterygoid.



TEXT-FIG. 3. *Parasuchus hislopi* Lyd. (×0·20). Restoration of the skull and mandible. *a*, lateral view of the skull; *b*, lateral view of the mandible; *c*, medial view of the mandible. For abbreviations, see text-fig. 2.

Palate (text-fig. 2). The palate is primitive with large palatal fenestrae, and is somewhat vaulted. Almost parallel with and in the vicinity of the mesial edge of the palatine, a low, rounded ridge is visible. Camp (1930) suggested that these ridges on either side were probably connected in life by a membranous sheath to form an incipient secondary palate. This soft palate would help in bringing a separate air passage well back along the palate. Dorsally the palatine, with the pterygoid behind, forms the floor of the orbit.

The choanae are placed slightly behind the external nares. The palatal ramus of the pterygoid extends considerably forward almost close to the choana. Posteriorly the transverse flange of the pterygoid curves ventro-laterally and is supported by the epipterygoid. The basipterygoid articulation consists of a smooth glenoid surface facing upwards and backwards, which curl around the basipterygoid process. The deep quadrate ramus is a thin sheet of bone and has a wing-like extension on either side to brace the medial surface of the quadrate.



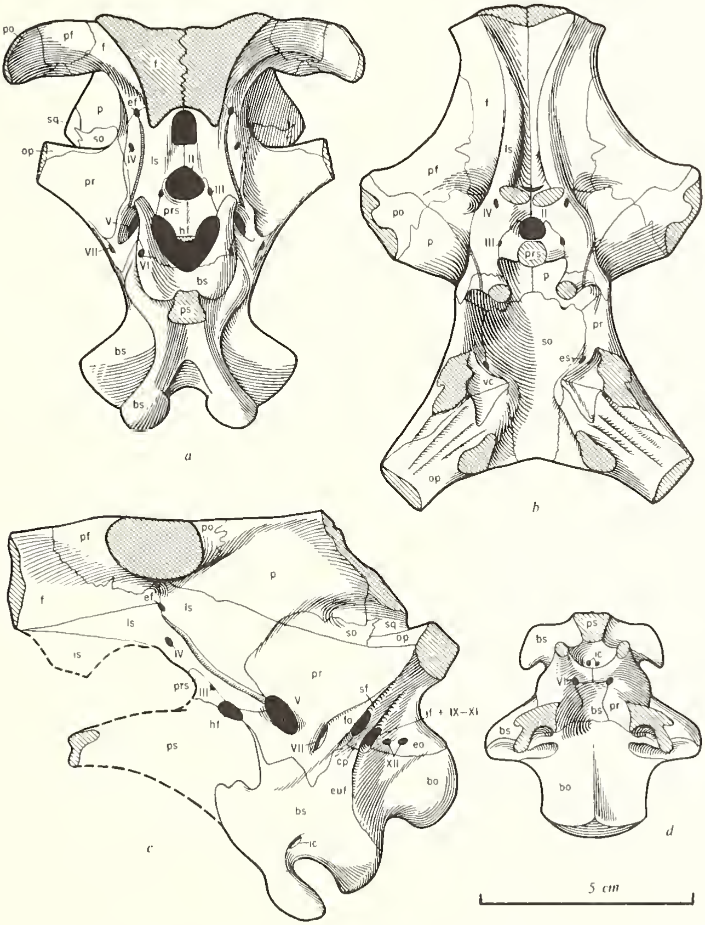
TEXT-FIG. 4. *Parasuchus hislopi* Lyd. (×0·20). Restoration of the skull and mandible. *a*, dorsal view of the mandible; *b*, occipital view of the skull; *c*, dorsal view of the skull (specimen ISI R 44 ♂). For abbreviations, see text-fig. 2.

Braincase (text-fig. 5). Six specimens display portions of the braincase of which ISI R 42, ISI R 44, and ISI R 160 are fairly complete and important for interpreting the detailed structure. An isolated basioccipital is represented by ISI R 45. The remaining two specimens are in the form of conjoined basioccipital-basisphenoid. A slight variability between the two sexes is observed.

The basioccipital shows a pair of basal knobs which abut against the basal tubera of the basisphenoid almost in a vertical plane. The knobs are connected by a small growth of bone which is usually concealed by the parasphenoid. Dorsally, the articular surfaces for the exoccipitals are rugose and slant ventro-laterally on either side of the mid-line.

The basal tubera of the basisphenoid are separated by a median notch and exhibit rugose muscle scars on the posterior faces. Anteriorly the basipterygoid processes are more slender than the tubera, and diverge as they descend from the anterior end. Each process shows a strong lateral facet for articulation with the palatal structure. Dorsally the basisphenoid exhibits the pituitary fossa or sella turcica behind which rises the dorsum sellae to join the pillars of the prootic on either side of the hypophyseal foramen. The long, sinuous dorso-lateral edge of the basisphenoid is capped by the prootic. Behind the dorsum sellae, a large basin-like depression is formed dorsally by the basioccipital and basisphenoid, lodging part of the mid-brain. Anteriorly and ventrally the basisphenoid supports the expanded base of the parasphenoid.

The parasphenoid is partly preserved as an extensive ventral ossification, sheathing



TEXT-FIG. 5. *Parasuchus hislopi* Lyd. (×0·56). Restoration of the braincase. *a*, anterior view; *b*, ventral view of upper portion; *c*, lateral view; *d*, dorsal view of the conjoined basioccipital-basisphenoid; specimen ISI R 44. For abbreviations, see text-fig. 2.

the conjoined basioccipital-basisphenoid. The base of the cultriform process is broken; anteriorly it extends as an elongated blade and slips into the interpterygoid vacuity. The presphenoid is represented by a tiny V-shaped bone hanging postero-ventrally from either side of the laterosphenoids. It separates the optic fissure from the hypophyseal foramen. The ventral stem is missing in the available specimens.

The laterosphenoids are large paired elements; each has two well-marked divisions —a mesial branch extending considerably forward below the skull roof, and a lateral branch curving downwards and backwards. The mesial branch encloses much of the olfactory tract. Ventrally the two sides meet each other and form the upper edge of the optic fissure. The interorbital septum is not represented in any specimens. Dorsally each branch articulates broadly with the frontal and barely touches the postfrontal by a serrate suture. Below the postfrontal, a pit is seen facing laterally for the reception of the epipterygoid. From this pit runs a longitudinal groove leading postero-ventrally into the prootic fenestra.

The lateral branch articulates with the parietal and prootic by dorsal and postero-ventral edges respectively. Internally it joins the supraoccipital. The prootic/laterosphenoid suture is extensive and runs between the prootic fenestra and the lateral opening of the hypophyseal fenestra. Antero-ventrally the bone supports the wing of the presphenoid.

The epiotics are indistinguishably fused with the laterosphenoids, supraoccipital, and prootics, and the demarcation of the bone is not possible.

The supraoccipital is a triangular plate, with a median ridge sloping postero-ventrally from the skull roof to cover the foramen magnum. At the summit of the plate is a rounded knob for articulation with the parietal. As the bone extends laterally it is sheathed by the parietal and the squamosal. On the inner surface of the side wall of the braincase, its junctions with the laterosphenoids and prootics are more extensive. Ventrally the bone lies upon the opisthotics and exoccipitals.

In the side wall of the braincase, each prootic is notched laterally by the large prootic fenestra. Anterior to it, a pillar-like process rises from the dorsum sella and is inserted into the laterosphenoid, and bridges the gap between the prootic fenestra and the hypophyseal foramen. Posteriorly each prootic is produced into a tapering process which overlaps the anterior part of the opisthotic to form the tympanic groove at its postero-ventral border.

The opisthotics have powerful paroccipital processes which abut against the downward hook of the squamosal. There are moderately developed ventral processes which separate the jugular foramen and fenestra ovale. A part of the stapes is found in one specimen (ISI R 47), slightly dislodged from the stapedial fossa.

The exoccipitals meet each other along the mid-line to form the floor and lateral wall of the foramen magnum. Just below its union with the supraoccipital a small projection is seen for the reception of the proatlas.

Braincase foramina. Various endocranial foramina and cavities preserved in our specimens give some information about the topography of the enclosed soft parts. The foramina provide passage for several important cranial nerves, and their positions and relationships can be ascertained when compared with those of closely related living reptiles.

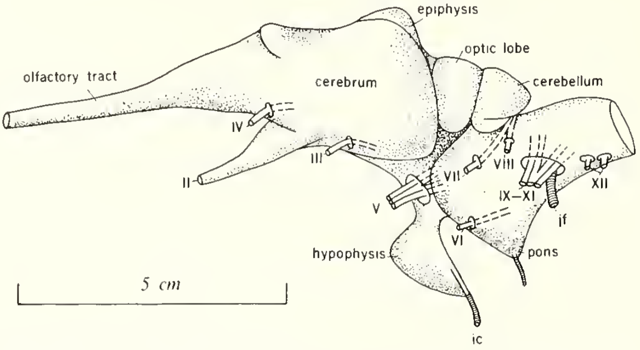
In front of the braincase, the large optic fissure is the exit of the optic nerve (II). Below this fissure, a pair of small pits conveyed the occulomotor (III), while above it lie a pair of small foramina for trochlearis (IV). The trigeminal (V) left the brain cavity through the prootic fenestra. A narrow longitudinal groove running upwards from the mouth of the prootic fenestra, indicates the course of the ramus opthalmicus. In the mid-line, just below the presphenoid, a narrow hypophyseal foramen can be seen. Below this foramen, the basisphenoid is excavated into a large pituitary fossa or sella turcica. Behind this, the dorsum sellae is pierced in the dorso-lateral parts by the external openings of the abducens (VI). Transversely through the sella turcica, the abducens nerve along with a pituitary vein and muscle slips possibly emerged through the lateral opening of the hypophyseal foramen into the orbit.

The openings of the canals for the internal carotid arteries are visible at the roots of the basipterygoid process; these openings tunnel through the bone in normal fashion and emerge at the base of the sella turcica through separate openings. Behind the prootic fenestra, a slit-like aperture on the side wall of prootic conveyed the facialis (VII); its palatine branch probably ran through a ventral groove and would take a forward course between the roots of the basipterygoid process. The foramen for the acousticus (VIII) is not visible in the Indian specimens, although Camp (1930) recognized it in *Machaeroprosopus* (= *Rutiodon*), in the suture between the prootic and paroccipital. The thin ridge-like crista paroccipitalis separates the fenestra ovalis from the jugular foramen. The jugular foramen lies between the otic capsule and the exoccipital; it probably transmitted nerves IX–XI, and a posterior branch of the jugular vein. The paired foramina at the base of each exoccipital are the outlets for the hypoglossal (XII).

Inner ear. The bony labyrinth (text-fig. 5) lodging the inner ear is enclosed within the prootic, opisthotic, and part of the supraoccipital bones. It comprises a large central vestibular cavity, encircled by three interconnected semicircular canals. The vestiblar cavity is rather triangular, mesially flattened, with its apices lying dorsally, anteriorly, and posteriorly respectively. It is mainly formed by the prootic and opisthotic. Proximate to its dorsal apex lies a small pit at the junction of supraoccipital and prootic for the endolymphatic sac.

The shape of the utriculus and sacculus cannot be judged with certainty from the bony contour of the vestibular cavity. The utriculus is likely to have been irregular triradiate structure as revealed from the triangular shape of the cavity. The sacculus may have been a rounded structure as is inferred from living reptiles. Below the vestibular cavity, the dorsal suture of the basioccipital/basisphenoid is excavated into a pair of pockets—the cochlear recesses for the reception of the lagenae. The close proximity of the fenestra ovalis to its cochlear recess indicates that the lagena was not elongate. Below the jugular foramen, the deep embayment on the basioccipital indicates the eustachian fossa, through which the eustachian tube connected the middle ear with the pharynx. In the middle-ear cavity, a low ridge separates the stapedial fossa from the tympanic fossa. The latter leads into a small tympanic foramen near the vestibular cavity.

Brain. Although the internal architecture of the fossil brains cannot be ascertained, it is possible to draw a number of conclusions from the cast of the brain cavity. The brain cavity of *Parasuchus* is extremely well preserved in specimen ISI R 44, permitting a partial reconstruction of the soft parts enclosed in the cavity. The brain of *Machaeroprosopus* (= *Rutiodon*), restored by Camp (1930), shows a slightly different flexure from this model. A cast in latex rubber of the brain cavity has been made and the major features are outlined here (text-fig. 6).



TEXT-FIG. 6. *Parasuchus hislopi* Lyd. (×0·7). Restoration of the brain, drawn mainly from a latex rubber cast of the cranial cavity; specimen ISI R 44.

Camp noticed that in *Alligator* the internal contours of the brain cavity reflect fairly closely the general topography of the brain, except in the region of the medulla oblongata which is considerably smaller in cross-section than the foramen magnum. This fact has been taken into account, and the medulla, in this reconstruction, is shown slimmer than the actual cavity.

Anterior to the medulla is a large ventrally projecting swelling, the pons varioli, uncommon in reptiles. The development of the pons, as interpreted by Camp, is due to heavy jaw muscles in parasuchians. The nerves innervating these jaw muscles have their centres in the pons. Farther forward, a second downward-dipping projection is the hypophysis which sinks vertically into the well-marked sella turcica.

The dorsal outgrowths of the cerebellum, optic lobes, and the cerebral hemispheres cannot be differentiated from the bony contours; their shapes and sizes shown in the model are conjectural, and are made from comparisons with *Alligator* (Romer 1956, fig. 14). The cerebral hemispheres lie in a position a little behind the orbit, and are connected to the olfactory bulbs by a slender isthmus of olfactory tract. The olfactory bulbs lie in an anterior position immediately behind the olfactory cavity. Below the olfactory tract, the optic nerve (II) runs forward almost parallel to it.

Although the pineal foramen is not present, the undersurface of the parietal in this region is hollowed out, presumably to accommodate the large epiphysis or pineal organ lying postero-dorsal to the cerebral hemispheres.

Mandible (text-figs. 3, 4). Passing backwards, the jaw increases in both depth and width. The alveolar border is fairly straight. A series of small nutrient foramina open on the outer surface of the dentary.

The coronoid is missing from the material at hand. Camp recognized this vestigial bone in *Machaeroprosopus* (= *Rutiodon*), loosely attached to the splenial and prearticular, but this element is usually lost in most specimens. The angular terminates beneath the glenoid. Dorsally the bone is excavated into a narrow longitudinal canal for lodging part of the meckelian cartilage. The surangular forms most of the lateral wall of the adductor fossa. The bone runs back, behind the glenoid, almost to the tip of the retroarticular process as a narrow end, where it is compressed between the articular and the angular.

The prearticular is preserved only by a fragment in our collection, and its relationships with the angular, coronoid, splenial, and articular are inferred from the sutural surfaces on the other bones. The articular is a short, compact bone, broadest at the glenoid region. The glenoid is not a single concavity, but it is rather saddle-shaped to receive the double keel of the quadrate condyle. This complex articulation must have limited the jaw to an essentially orthal movement. The glenoid is fairly deep, showing a general tilt towards the mesial side and is set transverse to the mid-line. From the glenoid, a flange of bone extends mesially as a narrow horizontal process and is pierced by a foramen for the chorda tympani branch of the facialis.

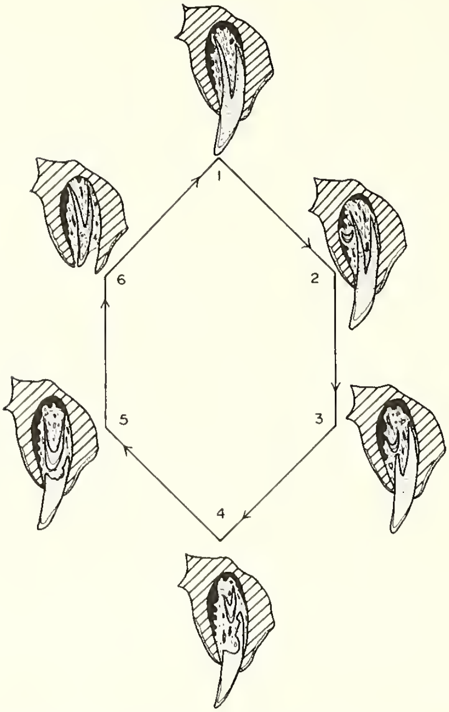
Dentition. This consists entirely of marginal teeth crowded in the premaxilla, maxilla, and dentary. The upper and lower posterior teeth are stout and elongate, compressed labio-lingually with the development of anterior and posterior carinae which are finely serrated. Contrary to this, the rest of the anterior teeth are slim, conical, and unserrated. The total dental count is fairly high and there appears to be forty-five teeth on either side of the skull, and about fifty-three teeth in each dentary. In a fully matured tooth, the relative length of the crown to the root is about 1:2·5.

Although repeated tooth-replacement activity has long been known to occur in parasuchians, our knowledge about the mode of replacing each individual tooth is, so far, poor. Fortunately, serial transverse sections of a tooth-bearing premaxilla in our collection exhibit all the various stages which would be expected in the replacement cycle of an individual tooth, and six stages are recognized (text-fig. 7).

Edmund (1960) described the wave-like replacement pattern of the relatively elongate conical teeth of parasuchians, the direction of this wave movement being apparently from back-to-front alternation in two series. The appearance of alternation in an 'odd' and 'even' series, however, is due to spacing of the impulses. A few excellent specimens in the ISI collections also show a clear sequence of back-to-front replacing waves, where the replacement teeth increase in size in alternate series towards the rear.

Post-cranial skeleton

Vertebral column. This consists of 25 presacrals, 2 sacrals, and more than 25 caudals. The centra are weakly amphicoelous throughout the series. The lengths of the centra show minor variations along the column, ranging from 3·3 cm to 3·8 cm. Cervicals are somewhat elongated, followed by a shortening of the centra in the anterior dorsals and a lengthening in the posterior dorsals. A serial change in the general build, as well as in the position of the rib facets, can be seen along the column.



TEXT-FIG. 7. *Parasuchus hislopi* Lyd. Dentition. Tooth replacement cycle of an individual tooth. Semi-diagrammatic, based on serial sections of a premaxilla. 1, the tooth is fully erupted, and the root is set in a deep socket. 2, the first indication of replacement activity is the appearance of a small calcified tooth germ in a shallow pocket in the alveolus lingual to the functional tooth. 3, a small erosion appears at the lingual side of the root of the functional tooth and the tooth germ migrates through it. 4, resorption of part of the lingual and labial sides of the root of the old tooth, and the replacing tooth enters within the pulp cavity of the predecessor to grow directly beneath the old crown. 5, further resorption of the root continues and the old tooth at this stage has been so much destroyed that its crown is held in position by a thin shell on the labial aspect; the developing tooth increases in size. 6, the shedding of the old tooth; the new tooth takes its position, and grows in size quite considerably in the socket and ready for eruption.

Atlas-axis complex. The proatlas was not found, but the exoccipital and the atlantal arch show distinct facets for the reception of this little bone. No ossified intercentra are found posterior to the atlas and axis. The atlas intercentrum is larger than the posterior one and has a typical crescentic form with its two ends clipped off to form articular facets for the neural arches. The neural arch halves of the atlas lack the spines and do not meet dorsally.

The three components of the axis, odontoid (= atlantal centrum), intercentrum, and the axis proper, remain separate in the Maleri specimens, these probably being juvenile forms. The neural arch of the axis is very large and distinctive, hatchetshaped, and elongated antero-posteriorly. The powerful spine was presumably used as an area of attachment by the obliquus capitis magnus muscle and the nuchal ligament connected to the head and vertebral column. The dorsal edge of the spine is not horizontal but slopes anteriorly and shows a rudimentary 'spine table' (Ewer 1965) at the back. The prezygapophysis of the axis is a little projecting flange, close to the horizontal, and facing upwards and outwards, the opposite of the normal situation. The post-zygapophysis, on the other hand, is oriented as usual. The transverse process is weakly developed.

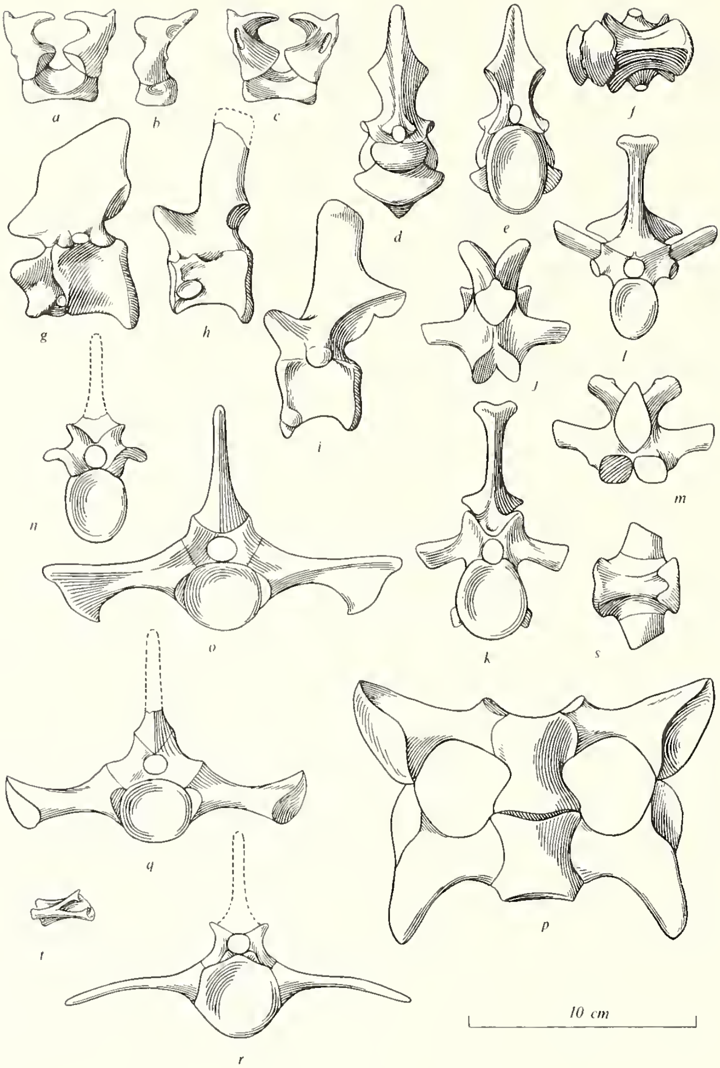
The movement of the skull appears to have been concentrated at the occipito-atlantal joint. Here the concavity of the atlas forms a universal ball and socket joint with the hemispherical condyle, and thus permits all the three types of movements: lateral, vertical, and rotary. All the three movements have approximately equal ranges but depend largely on how tightly the proatlas articulates with the skull, and on the elasticity of the joint capsule and vertebral ligaments (Evans 1939). In addition to this movement, the saddle joint between the atlas and axis would allow a good lateral motion, but vertical and rotary movements are limited. Moreover, the flat, practically horizontal, prezygapophysis of the axis would facilitate only lateral movement at this joint.

Presacral series (text-fig. 8). In this series there are possibly eight cervicals (whose ribs would fail to reach the sternum) and seventeen dorsals; the transition is gradual. The anterior cervicals are distinctly keeled mid-ventrally, but the keels gradually fade away moving backwards along the neck, and there is only a trace of them on the last cervical; behind that, there is no keel.

Rib facets are ubiquitous in the pre-sacrals, variably developed regionally. In the cervicals the parapophyseal facet lies ventrally close to the anterior rim of the centrum. A short distance above is the diapophysis at the tip of the transverse process, facing downwards and outwards. Passing backwards, the parapophysis gradually rises upwards in the cervicals and is half on the neural arch by the tenth vertebra. Behind this, the parapophysis entirely disappears from the centrum and is carried on the neural arch. The co-existence of separate parapophysis and diapophysis on the transverse process is retained throughout the succeeding dorsals, except the last one, where the para- and diapophyses are fused to a single articular facet (synapophysis) along the neurocentral suture, and the rib is co-ossified with the centrum.

The gradual shift of the diapophysis can also be seen. It is situated along the neurocentral suture in the cervicals, but gradually rises in the anterior dorsals and reaches the highest position in the mid-dorsal region, beyond which it descends again and ultimately lies on the neurocentral suture in the last two dorsals. The diapophyseal facet becomes enlarged from the anterior to mid-dorsal region, and the facet faces downwards in the anterior cervicals, slightly upwards in the anterior dorsals, and horizontally in the mid- and posterior dorsals.

The neural spine is compressed laterally and lies well towards the posterior half of the centrum. It is quite slim in the third vertebra, but further posteriorly the spines begin to elongate with a narrow base in the cervicals and posterior dorsals, but decline in height with a broad base in the anterior and mid-dorsal region. In the anterior dorsals, the spines become more and more expanded dorsally to form the spine



TEXT-FIG. 8. *Parasuchus hislopi* Lyd. (×0·30). Vertebral column. *a–c*, anterior, lateral, and posterior views of the atlas; *d–g*, anterior, posterior, ventral, and lateral views of the axis; *h*, lateral view of third vertebra; *i–k*, lateral, dorsal, and anterior views of eighth vertebra; *l*, *m*, anterior and dorsal views of fourteenth vertebra; *n*, anterior view of twenty-third vertebra; *o*, anterior view of first sacral; *p*, ventral view of the two sacrals; *q*, anterior view of second sacral; *r*, anterior view of twenty-eighth vertebra; *s*, ventral view of thirty-first vertebra; *t*, ventral view of thirty-ninth vertebra.

tables. Ewer (1965) suggested that the spine tables may be related to the attachment of muscles belonging to the transverso-spinalis system for raising the head.

The successive neural arches are jointed in amphiarthroses by zygapophyses of variable dimensions and orientations. In the cervicals from the third vertebra onwards, the prezygapophyses become greatly enlarged, and extend well forward beyond the anterior face of the centrum, but the facets again reduce in size in the dorsals. The slopes of the zygapophyses are generally close to 40° from the horizontal in the cervicals and anterior dorsals. Further backwards, the facets become more and more horizontally placed, but in the last presacral there is a sharp rise in the slope of the facets, similar to the cervicals.

Sacrum. The sacrum includes two separate vertebrae which are, in general, similar in build to those of the adjacent vertebrae, but possess distinctive large and wing-like ribs. Both the centra are equally long antero-posteriorly, and contact each other by almost flat surfaces. The zygapophyseal facets are moderately tilted. The neural spines are high and broad without any spine table. Rib facets are united to form the synapophysis, but the parapophysial and diapophysial facets can be distinguished, and are separated by the neuro-central suture. The parapophysis lies on the centrum and the diapophysis on the neural arch, facing each other at an obtuse angle.

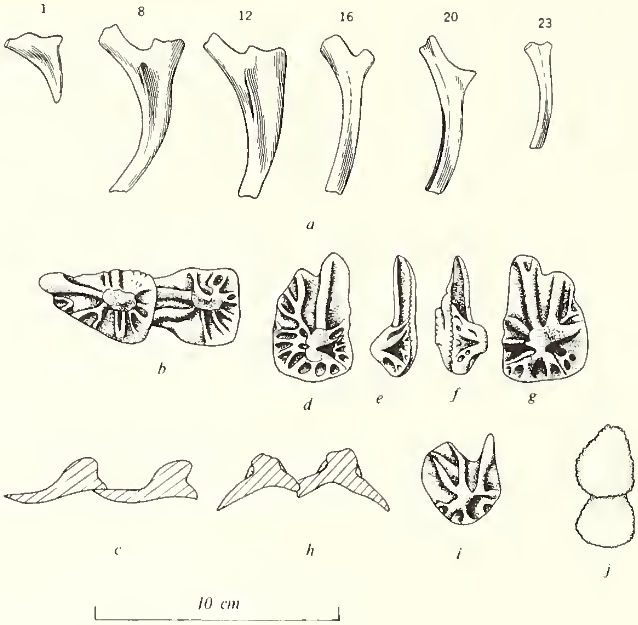
Caudals. The sacrals are followed by twenty-five caudals in the collection. Most of their spines and the zygapophyses are broken off. The serial changes in the caudals are reflected in the architecture of the centrum. The first two caudals are not very different from the preceding vertebrae. From the third caudal onwards, the centrum is more and more compressed laterally, and its height decreases. However, the length of the centrum remains steady up to the eighth caudal, beyond which the length is also diminishing, so that by the mid-caudal region, the centrum is narrow and spool-shaped. Further backwards, the caudals become slender and delicate.

The chevrons are Y-shaped and begin at the third caudal, and continue in gradually shortened form in the rest of the series. From the third caudal, each centrum bears a mid-ventral furrow, flanked by two strong ridges which terminate posteriorly in semicircular chevron facets.

Ribs. These are regionally differentiated (text-fig. 9). The cervical ribs are short and dichocephalous. Their heads remain close together in front, but the bifurcation of the head tends to increase posteriorly. The tubercular facet is larger than the capitular, but the latter is more prolonged medially. Just below the head a strong longitudinal ridge projects on the anterior surface of the shaft to which was presumably attached some of the medial bundles of the intercostal muscles.

The thoracic ribs are much longer and are curved. Each rib shaft is subtriangular proximally and subcircular distally. Proceeding backwards, the capitular attachment migrates upwards, and the heads tend to come closer to one another. In the posterior dorsals the two heads are united, but in the last dorsal, the rib is single headed and fused to the centrum.

The sacral ribs are immovably attached to the vertebrae, like the preceding dorsal and the succeeding caudals. Each rib is strong and stout, with a broad head, a short shaft, and a distal expansion applied to the inner surface of the ilium. The distal expansion is in the horizontal plane, and each rib extends towards its neighbour to make a slight contact at the tips. The first sacral rib takes the major share of the articulation with the ilium. The distal expansion of the second sacral rib is more prolonged antero-posteriorly; its posterior edge ends as a blade. A number of proximal caudals bear slightly curved short ribs, which are flattened dorso-ventrally and fused to the neural arches.



TEXT-FIG. 9. *Parasuchus hislopi* Lyd. (×0·33). *a*, anterior views of left presacral ribs of first, eighth, twelfth, sixteenth, twentieth, and twenty-third vertebrae. *b*, left paramedian dorsal scutes associated with fifth and sixth presacrals; *c*, the same, longitudinal section; *d*, left paramedian presacral scute, seventh; *e*, the same, mesial view; *f*, mesial view of right seventh presacral scute; *g*, the same, dorsal view; *h*, transverse section of the seventh paramedian pair; *i*, fifteenth presacral scute, left; *j*, left lateral scutes associated with seventh paramedian scute.

Dermal armour. Scutes are well preserved, having been found in almost their normal positions resting on their respective vertebrae. There are two rows of elongated paramedian scutes, supplemented laterally by small subcircular lateral scutes. The paramedian scutes are the better exhibited, extending throughout the column and undergoing various changes of size and shape (text-fig. 9).

The scutes are segmentally arranged; each vertebra bears a single paramedian pair, and each plate receives two lateral scutes. The lateral scutes are smooth and smaller in size than the paramedian. The length of the paramedian scute ranges from 2·5 cm to 5·0 cm. The cervical scutes, except the first one, are elongated, and the length decreases steadily in the posterior direction.

The paramedian scutes are coarsely sculptured dorsally. In each plate, there is an eccentric knob-like projection on the postero-medial quarter, from which an alternate series of ridges and furrows radiates towards the periphery. In the cervicals and anterior dorsals, each scute is triangular, but further posteriorly it is somewhat quadrate with a strong spine about 1·5 cm long, projecting anteriorly. The spine is abbreviated in the caudals.

Each scute overlaps its posterior successor. The ventral surface of the knob is deeply hollowed out to receive the tapering anterior portion of the succeeding scute. The juncture of the two scutes rests on the spine table.

The articulation between a paramedian pair is interesting. The left and right scutes in a pair are not perfect mirror images of one another; they differ considerably in the median hinge area. The mesial border of one of the pair is appreciably thickened as a flange, somewhat incised longitudinally. The mesial border of the antimere is sharp-edged and crenulated to fit into the incision of the flange. This groove-and-ridge joint permits a certain degree of movement, mainly flexion and extension along the hinge, but allowed no lateral movement. The ventral surface of the scute shows some scar marks.

There is an alternation of this interlocking device at the interval of two successive scutes. For example, in the first and second scutes, the flange develops on the left side, whereas the ridge is on the right side, but in the third and fourth, the reverse is the case, i.e. the flange develops on the right side and the ridge on the left side. This alternate pattern can be traced up to the eighteenth presacral, beyond which the scutes are somewhat fragmentary.

The ventral armour is unknown except in the throat region. Here a shield of small subcircular plates form a mosaic, interlocking by means of serrated borders or by overlapping. Each plate is 1·0–2·5 cm in diameter.

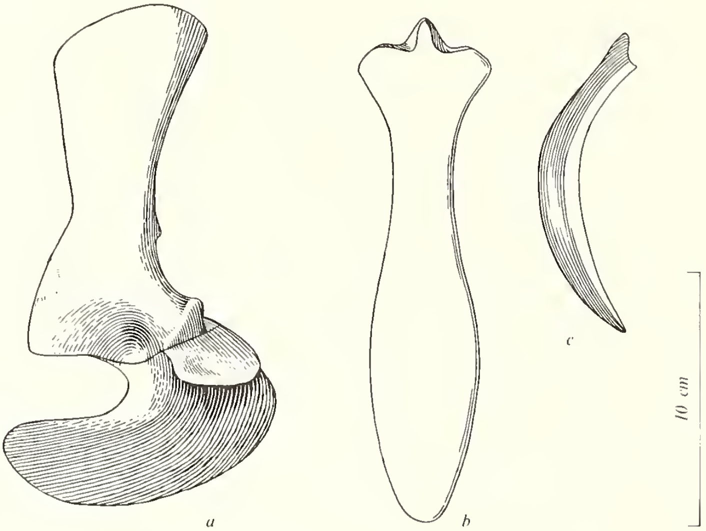
Abdominal ribs. A close-packed series of abdominal ribs was found in specimen ISI R 42, covering the posterior part of the belly. The abdominal ribs are arranged in a V-shaped form, just behind the interclavicle, in an overlapping series; the apex of the V points anteriorly. Each chevron is thick near the apex, where it is overlapped by its predecessor, but slim laterally where they are separate. The total count of the preserved part of the ribs may be as many as thirty.

Shoulder girdle (text-fig. 10). The scapula is curved so as to fit round the ribs. The main part of the blade is thin, but is appreciably thickened at the postero-lateral corner to form the glenoid. The glenoid lips face posteriorly and somewhat laterally, and diverge away from each other at an obtuse angle. A short distance above the glenoid is a prominence for the tendinous origin of the scapular head of the triceps muscle. At the anteroventral corner lies the acromion process to which the clavicle was connected by ligament.

The coracoid is a broad and short element, deeply emarginated anteriorly; the emargination was presumably closed in life by a bar of cartilage to form the coracoid foramen. Except for the glenoid region, the coracoid is otherwise thin, and fairly convex on the ventral surface.

The clavicle is a thin, crescentic bone. The dorsal end is a tapering process which abuts against the acromion process of the scapula. The shaft is curved, and bears a longitudinal ridge on the anterior surface. The distal end is thickened to a hook-like knob and shows the facet for the interclavicle.

The interclavicle is dagger-shaped; its anterior end is broad and trifurcated and bears antero-lateral notches in which the medial ends of the clavicles were lodged. The remainder of the bone is thin, slightly convex downwards, and tapers gradually posteriorly.

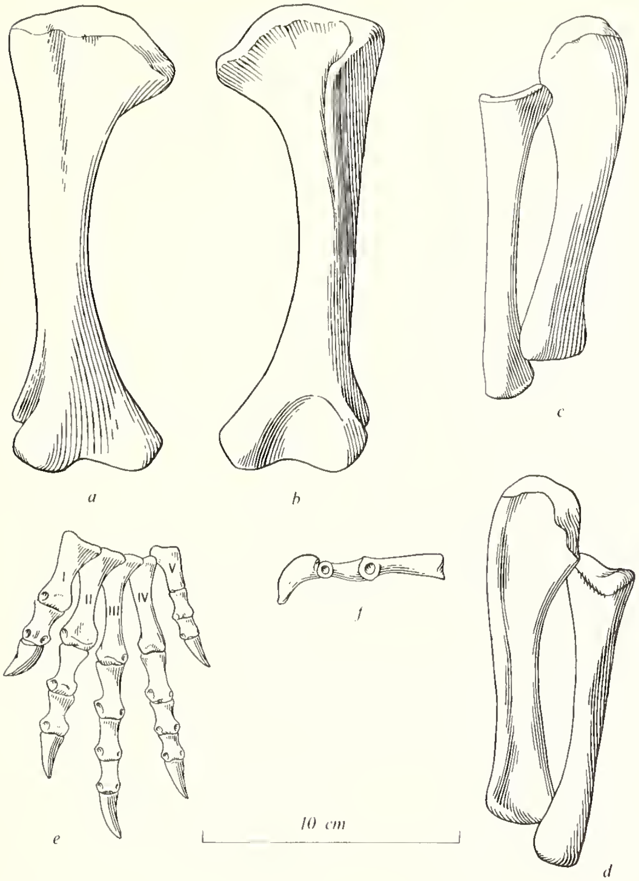


TEXT-FIG. 10. *Parasuchus hislopi* Lyd. (×0·33). Left shoulder girdle. *a*, scapulocoracoid, lateral view; *b*, ventral view of interclavicle; *c*, anterior view of clavicle.

Fore-limb (text-fig. 11). This is much shorter than the hind, the humerus being 76% of the length of the femur; when the lengths of the radius and tibia are added to the humerus and femur respectively, the same proportion is maintained. The propodials are distinctly longer than the epipodials; the length of the radius is 67% of that of the humerus, and the length of the tibia is 64% of that of the femur. The manus is considerably shorter than the pes; the first metacarpal is 60% of the length of the metatarsal.

The distal end of the humerus bears two convexities separated by a concave facet. The larger (anterior) convexity forms the capitellum, the concavity comprises the trochlea, and the smaller medial convexity affords an additional articular surface for the ulna. Near the capitellum lies the prominent epicondyle on the anterior border flanking a longitudinal groove for the passage of the radial nerve and the blood vessels.

The radius shows an oval and concave articular surface proximally to fit into the capitellum of the humerus, permitting a rotary motion. Laterally the head is prolonged as a lip to overlap the outer edge of the ulna, which is widely expanded proximally with a large olecranon process. The proximal articular end of the ulna slopes gently towards the radius to form a continuous surface for the articulation with the humerus. The distal end is swollen and oval in outline.

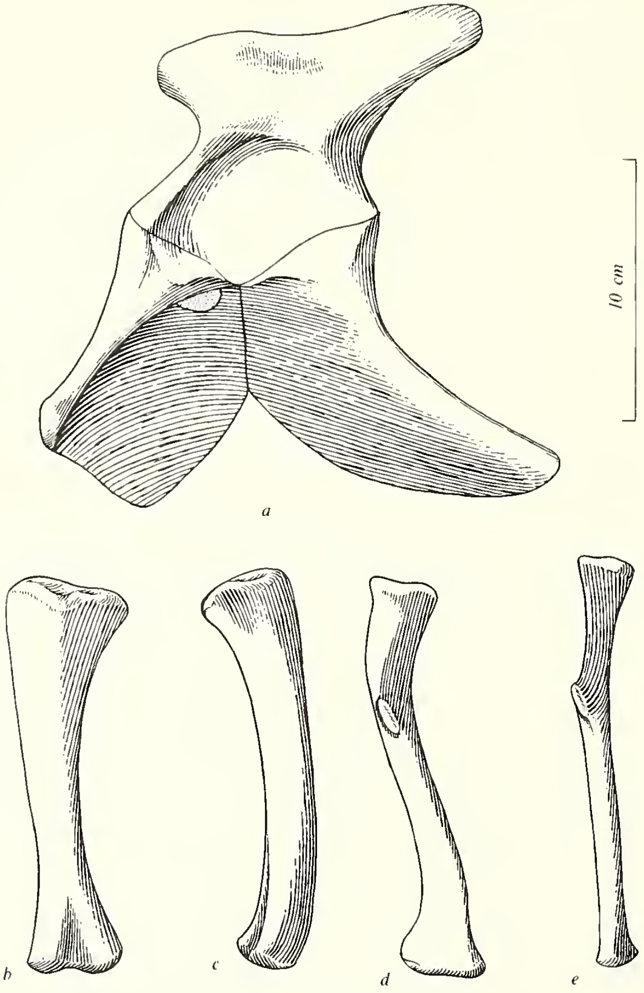


TEXT-FIG. 11. *Parasuchus hislopi* Lyd. (×0·33). Left fore-limb. *a*, *b*, dorsal and ventral views of humerus; *c*, *d*, anterior and posterior views of radius-ulna; *e*, restoration of the manus, dorsal view; *f*, left lateral view of the first toe.

No carpus was preserved, indicating that it might have been largely cartilaginous. No manus is entirely complete, but a composite can be made from the available specimens (text-fig. 11*e*). The metacarpals get progressively slimmer from the inner to the outer side of the hand. The phalangeal formula appears to be 2–3–4–5–3. The phalanges are all similar in form, although differing in size in the various digits. Each phalanx has a concave proximal facet and a convex distal facet, permitting a moderate amount of flexure. The claws are sharply pointed, recurved, and bilaterally compressed. They decrease in size laterally.

Pelvic girdle (text-fig. 12). The general structure of the pelvis is primitive and plate-like, V-shaped in cross-section, with an imperforate acetabulum. The median symphysis is rather straight, and is interrupted by a notch, presumably filled in life by symphyseal cartilage.

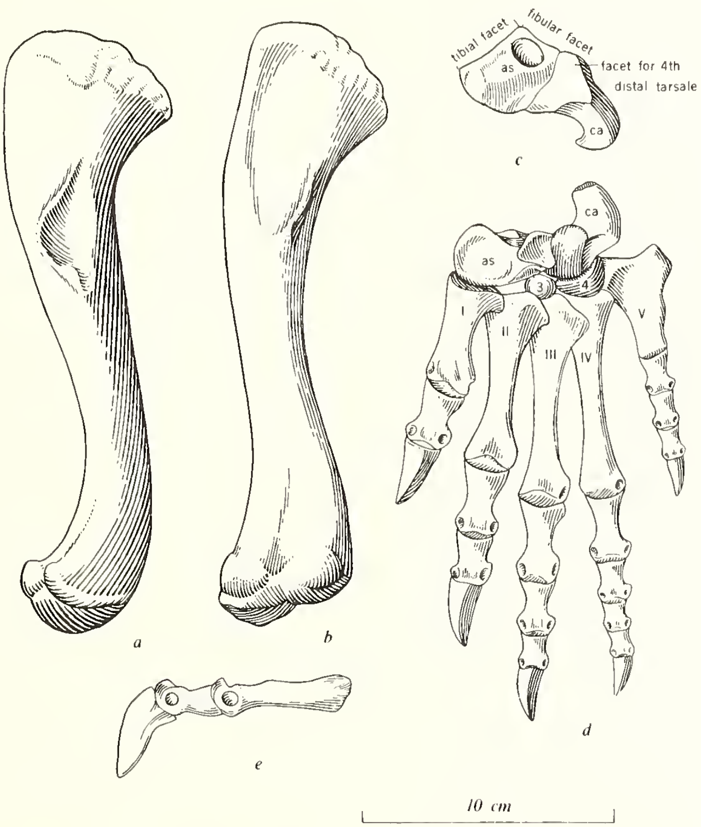
The ilium is an essentially vertical plate, roughly as long as high. The iliac crest is finely striated both externally and internally; the striations radiate out from the upper edge of the acetabulum towards the outer periphery. Internally the iliac crest is deeply concave lengthwise presumably to accommodate the longitudinal axial muscles. Below this, the incisions for the two sacral ribs are well marked. At the mid-height, the ilium is constricted to a neck. Here the anterior margin is appreciably thickened, but the posterior is sharp. On the antero-dorsal margin of the acetabulum, the supra-acetabular buttress is inflated laterally, and makes the acetabulum somewhat deep in the adjoining area, thus adapted to take strong forward thrusts from the femur.



TEXT-FIG. 12. *Parasuchus hislopi* Lyd. (×0·33). *a*, composite restoration of the left pelvis in side view; *b*, *c*, lateral and posterior views of left tibia; *d*, *e*, lateral and anterior views of left fibula.

The ischium is plate-like and extends posteriorly to the level of the prolongation of the ilium. The lamelliform anterior edge drops straight from the acetabulum to match the posterior edge of the pubis. The pubis is concave externally with an overhanging anterior rim. A large obturator foramen is located at the postero-dorsal corner through which the obturator nerve would pass to the muscles of the thigh. The pubic symphysis is short but deep.

Hind-limb (text-figs. 12, 13). The femur of *Parasuchus* is very reminiscent of that of a crocodilian. The bone is long and slender and shows a gentle sigmoid flexure. The proximal and distal expansions are rotated about 55° out of line with each other. The fourth trochanter rises as a ridge from the ventral surface of the femur, and is entirely confined to the proximal half of the femur. Medial to the fourth trochanter, a prominent muscle scar indicates the insertion of the coccygeo-femoralis longus. Distal to the fourth trochanter, a rugose projection can be seen on the postero-dorsal edge, more pronouncedly in specimen ISI R 42 (text-fig. 1). Camp (1930) interpreted this



TEXT-FIG. 13. *Parasuchus hislopi* Lyd. (×0·33). Left hind-limb. *a*, *b*, medial and ventral views of femur, composite restoration; *c*, antero-ventral view of astragalus-calcaneum; *d*, restoration of the pes, dorsal view; *e*, left lateral view of the first toe. Abbreviations: as, astragalus; ca, calcaneum; 3, 4, disal tarsals 3 and 4.

rugosity as a 'fifth trochanter' on which the ilio-femoralis possibly inserted by a tendon. The shaft is long and cylindrical and ovate in cross-section. Distally the two condyles are somewhat asymmetric, the lateral condyle is larger as well as extended farther distally than the medial one. The intercondylar groove is shallow.

The tibia has an expanded proximal end, triangular in section, and bears a weak cnemial crest. The distal end is slightly convex for the ankle joint and is ovate in outline. The fibula is a slim, antero-posteriorly compressed bone with slight sigmoid curvature. Both the proximal and distal ends are somewhat expanded transversely, connected by a twisted shaft. The prominent iliofibularis trochanter is an important landmark on the anterior face, running obliquely a little above the mid-height. Further distally the bone swells medio-laterally and becomes spatulate in shape. The distal end shows two separate facets for articulation with the tarsus; the medial one is apposed firmly to the upper surface of the astragalus, the lateral one is somewhat concave, and could move freely on a similar convex surface of the calcaneum.

The parasuchian tarsus, hitherto poorly known, is well represented in the Maleri specimens. It is of general crocodiloid pattern, differentiated into two rows, proximal and distal, and each row contains two elements. In the proximal row, the astragalus and calcaneum are entirely separate and fairly large in size. Proximally the astragalus rises as a dorsal apex, which separates two sloping facets for the crus. The tibial facet is larger, ovoid in outline, with a gentle concavity trending postero-medially into which the tibia fits firmly. The fibular facet is semi-elliptical, slightly depressed, and receives part of the distal end of the fibula; the rest of the latter meets the calcaneum. The postero-ventral surface is constricted to a 'neck', below which the lateral surface is slightly projected to form the spherical peg for the calcaneum. From the peg, the distal end curves medially into a convex arc for union with the metatarsals. Anteriorly an elongated pit is seen parallel to the rim of the fibular facet, probably for a ligament of the joint capsule.

The calcaneum has a narrow waist and two expanded ends. Dorsally the bone carries a convex sliding surface for the fibula. The mesial articular end is appreciably thickened and divides into two apposable surfaces for the astragalus. The anterior half has a convex condyle which laps around the neck of the astragalus, while the posterior half has a shallow socket which rotates on the peg of the astragalus. From this contact, the calcaneum is directed postero-laterally and terminates in a rugose tuber. The tuber lacks the posterior pulley-like groove as seen in typical crocodiles. Ventrally the bone is bevelled off at a flat triangular facet giving an intimate articulation with the lateral tarsale.

The medial distal tarsale is a small ovoid element, placed among the lateral distal tarsale, third metatarsal, and astragalus. The lateral distal tarsale is a large irregular bone, and contains separate articulating facets for the fifth metatarsal, the medial distal tarsale, and the ventral surface of the calcaneum.

The metatarsals increase in length but decrease in width from the first to the fourth, and the fifth is 'hooked'. Each metatarsal is well expanded at its proximal and distal ends, except the fifth metatarsal, whose distal expansion is not well pronounced. The fifth metatarsal is equal in length to the first one, and is Y-shaped. The medial branch of the Y bears a rectangular facet for articulation with the lateral distal tarsale. The lateral edge of the fifth metatarsal thickens ventrally to form the hamate process.

The phalangeal formula is 2–3–4–5–4. Each phalanx is expanded proximally and distally; the proximal surface is a shallow concave facet, the distal end forms a rolling hemicylindrical surface. Claws are present in all the digits, decreasing in length and proportion laterally. The length of the first claw is almost twice that of the fifth one. The medial surface of each claw is convex, the lateral surface bears a prominent longitudinal groove running almost the entire length.

The ankle joint of *Parasuchus*, although basically confirming to the crocodilian pattern, differs mainly on the nature of the astragalo-calcanear joint and the breadth of the tuber. The fit of the astragalus with the crus is so close and exact that it prohibits any movement between them. In *Parasuchus*, the initial phase in the evolution of the movable interlocking peg and socket joint between the astragalus and calcaneum can be seen. Here the astragalar peg is merely a gentle convexity and the calcanear socket is merely a shallow concavity. Nevertheless, this joint permits free rotary movements of the calcaneum on the astragalus. The astragalus forms part of the crus, whereas the calcaneum, distal tarsals, and the combined metatarsals move as a unit on astragalus and fibula. Thus the ankle joint is mesotarsal on the tibial side, and the crurotarsal on the fibular side.

Walker (1964) pointed out that the crocodiloid type of ankle joint seems to be a basic pattern in many thecodontians. Bonaparte (1971) recognized two distinct types of astragalo-calcanear joint among thecodontians, on the basis of the relative positions of peg and socket. One is 'crocodilian-normal' type, in which the peg is on the astragalus, and the socket on the calcaneum. The tarsus of *Parasuchus* is a good example of this pattern. The second category is the 'crocodilian-reversed' type, in which the peg is on the calcaneum and the socket on the astragalus. This pattern of ankle joint is found in *Riojasuchus*. It is interesting that both types of ankle joints allow rotary motion between astragalus and calcaneum, and both are well represented among the Late Triassic thecodontians.

STANCE AND GAIT

Charig (1972) analysed stance and gait in the archosaurs from the structural evidence of the pelvis and the hind-limb, and he recognized three distinct types, namely 'sprawlers' (the earliest Proterosuchia), 'semi-improved' or 'intermediate' (other Thecodontia and Crocodilia), and 'fully-improved' or 'vertical' (dinosaurs). *Parasuchus* seems to have possessed almost all of the attributes of the 'semi-improved' type, listed by Charig. These are: (*a*) two sacral vertebrae; (*b*) weakly developed anterior process of the ilium and weak supra-acetabular buttress; (*c*) imperforate acetabulum; (*d*) elongated pubo-ischiadic plate; (*e*) inturned head of the femur with sigmoid curvature of the shaft; (*f*) weakly developed fourth trochanter and absence of internal trochanter; (*g*) untwisted tibia; (*h*) flexible tarsus of crocodiloid pattern with peg and socket articulation between astragalus and calcaneum; (*i*) presence of calcanear tuber; (*j*) plantigrade pes with symmetrical pattern of toes.

The femur of *Parasuchus* resembles that of crocodilians very closely. There is a striking similarity in the limb proportions between *Crocodylus porosus* and *P. hislopi*. In both cases the length of the fore-limb as percentage of hind-limb is close to 80%.

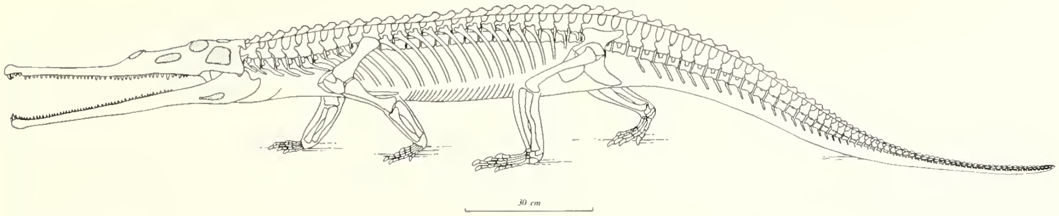
The crocodilians have three distinct gaits. There is a normal upright stance with body lifted off the ground, a gait most unlike the popular conception of a crocodile walking. When moving slowly, the body is dragged along the ground and the limbs are moved in a lizard-like fashion. More familiar is the tobogganing used when dashing into the water. The crocodile slides on its belly, using its legs as paddles. Cott (1961) observed an unusual method of locomotion by the young Nile crocodile, which gallops along with fore- and hind-limbs working together, like a bounding squirrel.

Walker (1970) pointed out that the elongated coracoids and the freeing of the shoulder girdle by the loss of the clavicles allow the lightly built juvenile Nile crocodile to gallop; but such locomotion could hardly have arisen in a large primitive thecodont like *Parasuchus*. Nevertheless all other crocodilian gaits were possibly used by *Parasuchus* without much difficulty. The ability of the crocodiles to raise the body off the ground may be associated with the extensive development of the pubo-ischio-femoralis externus and the adductor femoris (Romer 1923). These groups of muscles seem to have been well developed in *Parasuchus* also.

The limbs of *Parasuchus* are well built for terrestrial locomotion. Although the hind-limb is 24% longer than the fore-limb, its structure shows no bipedal adaptation. Unlike the archaic archosaurs, the humerus is but little twisted at its two ends. The glenoid lips face outwards and downwards, allowing the humerus to swing through an arc without dislocation. The humerus was swung in a rotary motion during a single stride, forwards and outwards, backwards and inwards.

The shaft of the femur is gently sigmoid, and its head, although it lies terminally, is turned inwards to some extent. The pelvis is V-shaped in end-view, where the median region of the elongated pubo-ischiadic plate recedes beneath the acetabulum. The articulation of the femur with the acetabulum indicates an oblique position of the femur. As Charig has pointed out, in this intermediate group (such as *Parasuchus*), the acetabulum, the sites of the origin of the protractor, and the retractor muscles and their insertion on the femur were no longer in the same plane. Hence, these groups of muscles not only pulled the femur anteriorly and posteriorly, but also towards the mid-line as a resultant component. The adduction of the femur would help the animal to raise the body off the ground, particularly during rapid progression. Thus *Parasuchus* was certainly incapable of adopting a vertical posture, but had improved its posture from the typical sprawling position to a great extent.

The 'twin' specimens of *Parasuchus*, being articulated, give valuable information as to the position and attitude of the different bones. The skull is 585 mm long, the presacral vertebral series in natural association is 900 mm, and the preserved part of the tail would also be 900 mm. The tail may have been somewhat longer, say about 1200 mm. The estimated snout to tail-tip length of the restored skeleton, representing an individual of the size of ISI R 42, would be about 2·7 m. Text-fig. 14 shows a restoration of the whole skeleton, with the animal using this suggested quadrupedal gait with the body off the ground.



TEXT-FIG. 14. *Parasuchus hislopi* Lyd. Restoration (× 0·06).

MODE OF LIFE

The active carnivorous habit of *Parasuchus* is reflected in the gastric contents of the 'twin' specimens, where both the hunter and the hunted were fossilized in the same block. Each specimen contains a small bipedal archosaur in the stomach, the bones of which are more or less articulated and well preserved, except for the cranial region. The left specimen (ISI R 42), in addition to this, shows a few skull bones of a rhynchosaur in its stomach. The general skeletal construction of *Parasuchus* must be considered in relation to this mode of life, and the habits of recent crocodilians could be taken as an analogy, assuming *Parasuchus* occupied an ecological niche like that of living crocodilians.

Most revealing of all anatomical evidence, of course, is the dentition. The numerous sharp-pointed conical and polyphyodont teeth are that of a formidable carnivore. The teeth do not meet at the tips, but interdigitate when the jaws are closed. The elongated jaws with sharp teeth and wide gape are well suited for prehension. The frontal position of the eyes close to the mid-line, with a fairly large degree of binocular vision must have a good correlation with predacity. The crocodilians have about 25° of binocular vision (Walls 1963), and *Parasuchus* would have had close to this value, as is inferred from the similar position of the orbit. Binocular vision offers good distance judgement which enables the killer to strike the prey more precisely.

With the eyes and nostrils set high in the skull, *Parasuchus* had a natural advantage over its prey at the water's edge, as it could lie totally submerged. Thus lying in the water, it could breathe, smell, and see. The development of a soft secondary palate would help air breathing while seizing prey under water. Once the jaws got a firm hold on the animal, the twist would be an effective way of overpowering the prey. The slender snout is a special device for catching swift-swimming fishes by a sidewise sweep of the head.

Like all other predators, the parasuchians also had powerful jaw muscles (Anderson 1936). The opening and closing of the jaw must be very rapid in a snapping action. The forwardly sloping pterygoideus allowed the lower jaw to snap shut rapidly from the fully open position, for seizing prey. When the prey was caught between the jaws, a strong bite would be essential to kill it. This was performed by the vertical temporalis muscle. These two sets of muscles must have been well developed in *Parasuchus*, as is evident from the architecture of the skull.

The food remains inside the stomach of *Parasuchus* give some clue as to its method of feeding. The skull bones of the medium-sized rhynchosaur are found somewhat scattered in the stomach, whereas the little bipedal archosaur is preserved almost in natural articulation, except for the skull. This evidence indicates that, if the prey was small, it was gulped down whole; if the prey was too large to be swallowed whole, it was reduced to pieces. Possibly small prey was orientated head first to make it easier to swallow, after crushing the skull. The animal hunted actively, rather than ambushing its prey from a place of hiding.

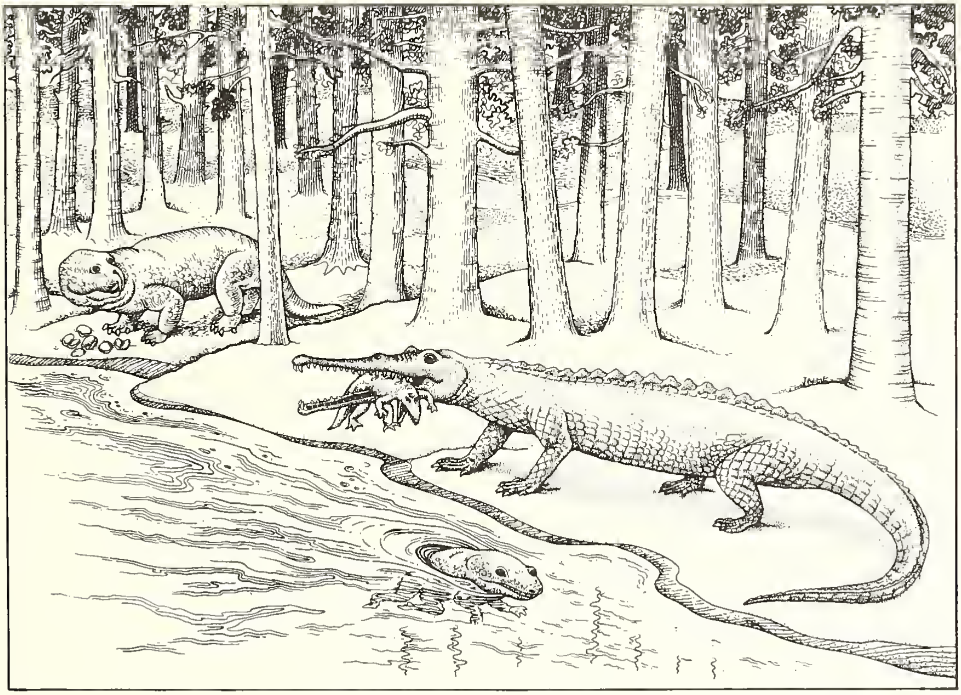
The limbs of *Parasuchus* are well built for terrestrial locomotion. The fore-limbs being slightly shorter than the hind, are well adapted for grasping and holding the prey with sharp claws. The animal was probably capable of a rapid chase for a short distance. The relatively large and spreading manus and pes may have helped to prevent the feet sinking into the swampy land which was the probable habitat. The throat and back of the animal are protected by a formidable shield of scutes, making it almost impregnable. The abdominal ribs provide reinforcement for the belly. During swimming, the limbs would probably be folded against the body and the powerful, compressed tail used for sculling through the water. The latter could strike an assailant a severe blow by a sidewise sweep.

What was the mode of life of *Parasuchus* in the Maleri ecosystem? The physical setting in which the animal lived seems to be broad flood plains of low relief with swamps and numerous large rivers. The climatic conditions were probably of monsoon type, marked by high rainfall with alternate wet and dry seasons (Robinson 1971). There are a few records of contemporary flora, mainly as fragments of *Dadoxylon*, *Araucarioxylon*, and *Mesembrioxylon* (Pascoe 1959, p. 971). The animal presumably lived for the most part in the water, seeking food and lowered body temperature, and making only occasional excursions on to the ground, particularly during egg-laying. Sunny banks would be a favourite spot for hunting the land-dwellers, particularly when the latter came to water for drinking or feeding. *Parasuchus* in the Maleri environment seems to have been the arch predator of his time, having little to fear from the enemies, and thus enjoyed a brief period of supremacy and success (text-fig. 15).

DISTRIBUTION, EVOLUTION, AND RELATIONSHIPS OF THE PARASUCHIDAE

Parasuchian phylogeny is a good example of explosive evolution during the Late Triassic. The continental deposits of North America, Europe, and India have provided a variety of parasuchians with excellent cranial material and a number of relatively complete skeletons. Parasuchian remains from North Africa, China, and Madagascar are at present insufficiently known for comparative study or diagnosis. The great multiplicity of generic names for parasuchians has been reduced to a few after careful evaluation (Gregory 1962, 1969; Gregory and Westphal 1969). Gregory's classification is more simple and realistic, as parasuchians are a morphologically homogeneous group of limited stratigraphic range, in the sense that they have a restricted number of variations from a basic pattern.

Gregory recognized five valid genera: *Paleorhinus*, *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, and *Rutiodon*. He considered *Francosuchus* as a subgenus of *Paleorhinus*, and *Parasuchus* as a synonym of *Nicrosaurus*. However, the present study, amplified



TEXT-FIG. 15. Restoration of the Upper Triassic Maleri landscape showing some of the characteristic tetrapods. In the water is the labyrinthodont amphibian *Metoposaurus*. Behind it is the predatory parasuchian *Parasuchus* holding a bipedal archosaur in its mouth. On the left, is the rhynchosaur *Paradapedon* eating mussels (unionids, *Tikhia*). In the background is shown *Araucarioxylon* forest. These animals lived in a lowland environment near the water's edge, in a subtropical climate with alternate hot and dry seasons, and a high rainfall.

by excellent material, indicates a somewhat different picture. In this study the generic status of *Parasuchus* and *Francosuchus* is revived, and *Paleorhinus* is considered as a subjective junior synonym of *Parasuchus*. The arguments for this revised classification will follow immediately after brief descriptions of the known parasuchian genera. The classification presented herein is based mostly on skull characters and will enable identification of skull material rather precisely (adapted from Case 1922, Camp 1930, and Gregory 1962). Differences certainly exist in the post-cranial structures, but their use in classification is severely hampered by lack of association of parts in most genera. Among various post-cranial characters, the nature of scutes (whether overlapping or not) is singled out as being of great phyletic significance.

Systematic Descriptions

Order THECODONTIA
Suborder PARASUCHIA
Family PARASUCHIDAE Lydekker, 1885

Long-snouted carnivorous reptiles from the Late Triassic continental sediments of Europe, India, and North America. A good familial diagnosis is given by Gregory (1962). *Mesorhinus* from the Early Triassic of Germany may be the earliest member of the family, although Gregory doubted its affinity, age, and provenance.

Subfamily PARASUCHINAE Lydekker, 1885
Genus PARASUCHUS Lydekker, 1885

Distribution. India, North America.

Type species. Parasuchus hislopi Lydekker, 1885; Maleri Formation, India.

Small to medium-sized, skull length 600–900 mm, rostrum slender and short without crest; low rostral ratio (1·0–1·2); external nares lie well in front of the antorbital fenestrae, internal nares behind external nares; squamosals abruptly truncate without any posterior process; supratemporal fenestrae at the level of the skull roof; large interpterygoid vacuity; teeth short and slender.

Subgenus PARASUCHUS Lydekker, 1885

Parasuchus hislopi Lydekker, 1885; Maleri Formation, India.

Moderately deep skull, orbit directed outwards and upwards; post-temporal fenestrae moderate sized; teeth weakly heterodont; overlapping scutes.

Subgenus PALEORHINUS Williston, 1904

Paleorhinus bransoni Williston, 1904; Popo Agie Formation, Wyoming, North America.

Low occiput, orbit directed more upwards than outwards; small post-temporal fenestrae; homodont dentition, non-overlapping scutes.

Genus ANGISTORHINUS Mehl, 1913

Distribution. North America.

Type species. Angistorhinus grandis Mehl, 1913; Popo Agie Formation, Wyoming, North America.

Large-sized, skull length 900–1200 mm; moderately deep; external nares posterior, between the antorbital fenestrae; post-temporal arcade at the level of the skull roof; rostrum long and strong with prominent downturned tip and lacks crest; rostral ratio moderate (1·4–1·9); large infratemporal and post-temporal fenestrae; palate vaulted with small interpterygoid vacuity; squamosal process rounded and short, extended well behind the contact of the paroccipital process; orbits directed outwards as much as upwards; teeth weakly heterodont with compressed and enlarged posterior teeth; non-overlapping scutes.

Genus NICROSAURUS Fraas, 1866

Distribution. Germany and North America.

Type species. Nicrosaurus kapfi (Meyer), 1860; Stubensandstein, Stuttgart, Germany.

Moderate to large sized, skull length 750–1400 mm; moderately deep; massive rostra with continuous rostral crest; rostral ratio low (average 1·2), independent of size; external nares posterior, between the antorbital fenestrae; squamosal process short and deep; narrow interpterygoid vacuity; post-temporal fenestrae large, supratemporal fenestrae depressed; strong heterodont teeth, overlapping scutes.

Genus RUTIODON Emmons, 1856

Distribution. Europe and North America.

Type species. Rutiodon caroliensis Emmons, 1856; Cumnock Formation, North Carolina, U.S.A.

Large-sized, skull length 800–1200 mm, rostra vary from slender and uncrested in small skulls to moderately robust with large dorsal crests in the posterior half of the largest individuals; rostral ratio low to moderate (1·2–1·7); squamosal process slender and show phyletic elongation; external nares posterior, between antorbital fenestrae; supratemporal fenestrae depressed; interpterygoid vacuity narrow, large post-temporal fenestrae; orbits directed obliquely outwards and upwards; strongly heterodont teeth; non-overlapping scutes.

Subfamily MYSTRIOSUCHINAE von Huene, 1915

Genus FRANCOSUCHUS Kuhn, 1932

Distribution. Germany.

Type species. Francosuchus broilii Kuhn, 1932; Blasensandstein, Franconia, Germany.

Small-sized, skull length 600 mm; extremely low occiput; rostrum slender and long without crest; moderate rostral ratio (1·7); external nares anterior to antorbital fenestrae but more close to orbits than in *Parasuchus*; posterior squamosal process absent; orbit directed more upwards than outwards; large interpterygoid vacuity, post-temporal fenestrae small; supratemporal fenestrae at the level of the skull roof; homodont dentition; non-overlapping scutes.

Genus MYSTRIOSUCHUS Fraas, 1896

Distribution. Germany.

Type species. Mystriosuchus planirostris (Meyer), 1863; Stubensandstein, Würtemberg, Germany.

Small to medium-sized, skull length 750–1050 mm, fairly deep; highly specialized posterior nares close to orbit resulting in high rostral ratio (2·2–2·7); rostrum low and slender with occasional dorsal swellings; greatly depressed supratemporal fenestrae close to paroccipital process; orbit directed more outwards than upwards; squamosal primitive, lacking posterior process; teeth slender and homodont; small interpterygoid vacuity; post-temporal fenestrae extremely reduced.

GENERA INCOMPLETELY KNOWN

Genus MESORHINUS Jaekel, 1910

Type species. Mesorhinus fraasi Jaekel, 1910; Buntsandstein, Germany.

Possibly the earliest parasuchian; low occiput; external nares lie well in front of the antorbital fenestrae; pineal foramen present; supratemporal fenestrae at the level of the skull roof; palate primitive with large interpterygoid vacuity.

Horizon, supposedly Lower Trias, highly dubious (Gregory 1962). The only specimen was lost during the Second World War.

Genus PACHYSUCHUS Young, 1951

Type species. Pachysuchus imperfectus Young, 1951; Lower Lufeng Series, Yunnan, China.

Very fragmentary material, lacks diagnostic characters.

Good skeletons of parasuchians have recently been discovered from Triassic sediments of Morocco, North Africa. No descriptions or affinities are yet available.

Analysis of Characters

Gregory (1962, Table 1) has analysed various skull characters in detail and tabulated to those, which, according to him, are of great systematic value. He did not include *Parasuchus*, as the Indian material was then poorly known. A slightly modified and more elaborate version of Gregory's scheme is given below (Table 3).

Some of the morphologic characters such as skull height, direction of the orbit, and size of the post-temporal fenestra, may be affected by crushing, and thus should be used with some caution. The following characters seem to be of great systematic value; some of the characters are indicative of grades of evolution, some are of phyletic affinity.

1. Position of external nares in relation to antorbital fenestrae; more precisely, the distance between the nares and the orbits.
2. Rostral ratio (pre-narial to post-narial length); nature of the rostrum, whether slender, robust, crested, or uncrested.
3. Posterior border of the supratemporal fenestrae at the level of the skull roof, or depressed.
4. Presence or absence of the posterior squamosal process.
5. Palate open or vaulted.
6. Teeth homodont or heterodont.
7. Scutes overlapping or non-overlapping.

Parasuchus, *Paleorhinus*, and *Francosuchus* share many of the primitive characters and represent more or less similar levels of organization. *Parasuchus* and *Paleorhinus* are so similar in form that their generic distinction is questionable. Of twelve cranial

TABLE 3. Tabular comparisons of diagnostic characters of parasuchid skulls.

	Paleorhinus	*Francosuchus*	*Parasuchus*	*Angistorhinus*	*Mystriosuchus*	*Nicrosaurus*	*Rutiodon*
I. Position of external nares	Anterior	Anterior	Anterior	Posterior	Posterior	Posterior	Posterior
II. Position of orbit	Directed more upwards than outwards	Directed more upwards than outwards	Directed outwards as much as upwards	Directed outwards as much as upwards	Directed upwards and backwards	Obliquely more outwards than upwards	Obliquely more outwards than upwards
III. Nature of supratemporal fenestra	Level of the skull deck	Level of the skull deck	Level of the skull deck	Level of the skull deck	Greatly depressed	Depressed	Depressed
IV. Nature of infratemporal fenestra	Small, posterior to orbit	Small, posterior to orbit	Small, posterior to orbit	Large, at the level of the orbit	Small, posterior to orbit	Large, at the level of the orbit	Large, at the level of the orbit
V. Nature of post-temporal fenestra	Small	Small	Moderate	Large	Very small	Large	Large
VI. Pineal foramen	Present (only in *P. scurriensis*)	Absent	Absent	Absent	Absent	Absent	Absent
VII. Nature of interpterygoid vacuity	Large	Large	Large	Small	Small	Small	Small
VIII. Ratio of rostral length to postnarial length	1·0–1·2 Low	1·7 Moderate	1·1 Low	1·4–1·9 Moderate	2·2–2·7 High	1·05–1·37 Low	1·2–1·7 Low to moderate
IX. Ratio of skull height to skull width	0·37 Low	0·30 Low	0·57 Moderate	0·44 Moderate	0·63 High	0·44 Moderate	0·63 High
X. Posterior squamosal process	Absent	Absent	Absent	Rounded, short	Absent	Rounded, elongate	Rounded, elongate
XI. Plane of quadrate	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Vertical	Vertical	Vertical
XII. Dentition	Homodont	Homodont	Weakly heterodont	Weakly heterodont	Homodont	Strongly heterodont	Strongly heterodont

TABLE 3. Tabular comparisons of diagnostic characters of parasuchid skulls.

	Paleorhinus	*Francosuchus*	*Parasuchus*	*Angistorhinus*	*Mystriosuchus*	*Nicrosaurus*	*Rutiodon*
I. Position of external nares	Anterior	Anterior	Anterior	Posterior	Posterior	Posterior	Posterior
II. Position of orbit	Directed more upwards than outwards	Directed more upwards than outwards	Directed outwards as much as upwards	Directed outwards as much as upwards	Directed upwards and backwards	Obliquely more outwards than upwards	Obliquely more outwards than upwards
III. Nature of supratemporal fenestra	Level of the skull deck	Level of the skull deck	Level of the skull deck	Level of the skull deck	Greatly depressed	Depressed	Depressed
IV. Nature of infratemporal fenestra	Small, posterior to orbit	Small, posterior to orbit	Small, posterior to orbit	Large, at the level of the orbit	Small, posterior to orbit	Large, at the level of the orbit	Large, at the level of the orbit
V. Nature of post-temporal fenestra	Small	Small	Moderate	Large	Very small	Large	Large
VI. Pineal foramen	Present (only in *P. scurriensis*)	Absent	Absent	Absent	Absent	Absent	Absent
VII. Nature of interpterygoid vacuity	Large	Large	Large	Small	Small	Small	Small
VIII. Ratio of rostral length to postnarial length	1·0–1·2 Low	1·7 Moderate	1·1 Low	1·4–1·9 Moderate	2·2–2·7 High	1·05–1·37 Low	1·2–1·7 Low to moderate
IX. Ratio of skull height to skull width	0·37 Low	0·30 Low	0·57 Moderate	0·44 Moderate	0·63 High	0·44 Moderate	0·63 High
X. Posterior squamosal process	Absent	Absent	Absent	Rounded, short	Absent	Rounded, elongate	Rounded, elongate
XI. Plane of quadrate	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Inclined, sloping posteriorly	Vertical	Vertical	Vertical
XII. Dentition	Homodont	Homodont	Weakly heterodont	Weakly heterodont	Homodont	Strongly heterodont	Strongly heterodont

characters listed by Gregory as typical of *Paleorhinus*, eight are also found in *Parasuchus* (see Table 3). Four contrasting characters between these two forms are: (*a*) Skull-height, low in *Paleorhinus* but moderate in *Parasuchus*. (*b*) Size of the post-temporal fenestrae—small in *Paleorhinus* but moderate in *Parasuchus*. (*c*) Position of the orbit; directed more upwards than outwards in *Paleorhinus*, but in *Parasuchus*, it is directed outwards as much as upwards. (*d*) Dentition: homodont in *Paleorhinus* but weakly heterodont in *Parasuchus*.

Of these, the first three characters, as has already been pointed out, may easily be accounted by differential crushing and individual growth differences. It is thus seen that the only distinction between *Paleorhinus* and *Parasuchus* hinges mainly on the nature of the dentition. Otherwise *Paleorhinus* and *Parasuchus* are remarkably similar in all qualitative features of narial form and position and development of temporal arcades (text-fig. 16). The beginning of the differentiation of teeth in *Parasuchus* is a derived character and indicates that *Parasuchus* is just one step further forward than *Paleorhinus*. Uniting *Paleorhinus* and *Parasuchus* in a single genus stresses the close relationship between these animals; their separate identities at subgeneric level seem to be a useful compromise between two geographically separated populations. In this connection it is interesting to mention that the Indian metoposaur, *Metoposaurus maleriensis* from the same horizon, is extremely similar to those of North America and Germany, differences being at a specific level only (Roy Chowdhury 1965).

Although *Francosuchus* agrees well with *Parasuchus* (*Paleorhinus*) in most of the cranial characters, the outstanding feature of *Francosuchus* is its extremely long and slender snout. The high rostral ratio is weighted heavily in phyletic classification of parasuchians. This is why *Francosuchus* is kept separate as a distinct genus from *Parasuchus* (*Paleorhinus*).

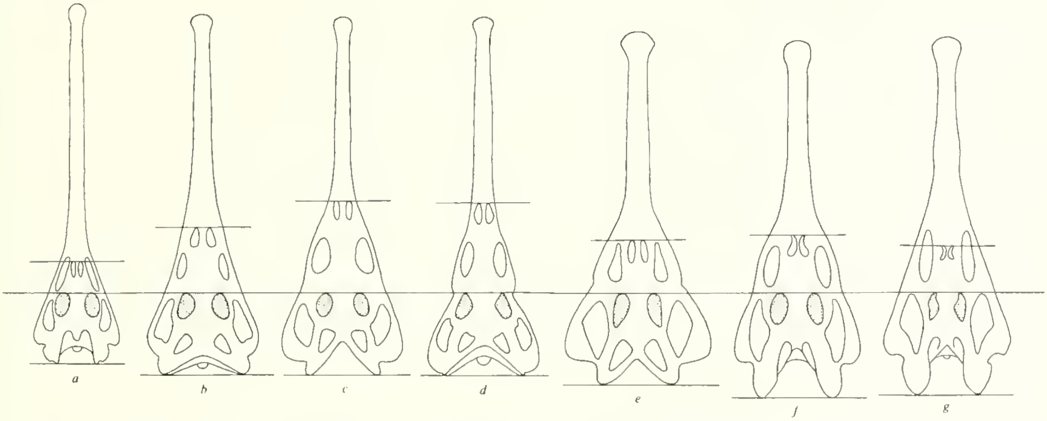
Phenetic Relationships

The parasuchian genera, when arranged in order of chronology, show certain changes in cranial characters. From the primitive *Parasuchus* (*Paleorhinus*)-like animal, the morphologic changes shown by the Parasuchidae could have appeared by the following evolutionary developments:

1. Gradual posterior shift of the external nares in relation to antorbital fenestrae.
2. Change of the orientation of the orbit from upwards to more outwards.
3. Gradual depression of the supratemporal fenestra from the skull deck to the occipital region.
4. Progressive anterior enlargement of the infratemporal fenestra.
5. Gradual enlargement of the post-temporal fenestra.
6. Loss of the pineal foramen.
7. Reduction in size of the interpterygoid vacuity.
8. Gradual increase of the rostral ratio (correlated to 1).
9. Progressive increase of the height of the skull in relation to its width.
10. Gradual enlargement of the squamosal process posteriorly.
11. Swinging forward of the quadrate, the backwardly sloping quadrate becoming vertical.
12. Tooth differentiation, from homodont to heterodont.

One should take into account the morphological variations that result from differences in sex and age. It is not unlikely that some of the above changes could have been produced by these two factors. Nevertheless, the general pattern of evolution can be gathered from an analysis of these characters.

It appears from the Table 3 that the parasuchian genera tend to segregate into three different stages or grades of evolution from the primitive to the advanced condition. The primitive grade of greatest paleotelic weight includes the genera *Francosuchus* and *Parasuchus. Angistorhinus* is intermediate in grade as its nostrils have shifted fairly far back between the antorbital fenestrae, with the development of the posterior squamosal process. *Nicrosaurus*, *Mystriosuchus*, and *Rutiodon* are advanced, in that the supratemporal fenestrae greatly depressed below the skull roof (text-fig. 16).



TEXT-FIG. 16. Dorsal views of parasuchian skulls to show variations in the position of the external nares, antorbital fenestrae, supra- and infratemporal fenestrae, and posterior squamosal process; the skulls have been reduced to a unit length for comparisons. Orbit stippled. *a*, *Mystriosuchus planirostris* (after McGregor 1906); *b*, *Francosuchus broilii* (after Kuhn 1936); *c*, *Paleorhinus* sp. (after Gregory 1969); *d*, *Parasuchus hislopi*; *e*, *Angistorhinus megalodon* (after Gregory 1969); *f*, *Nicrosaurus kapfi* (after Gregory 1969); *g*, *Rutiodon adamanensis* (after Camp 1930).

Phylogenetic Relationships

It is very difficult to derive the long-snouted parasuchian from any other families of Thecodontia, since intermediate forms are lacking. Walker (1968) suggested that *Proterochampsa* from the Ischigualasto Formation of Argentina is a primitive parasuchian. Romer (1971) also described a further two closely related forms, *Chanaresuchus* and *Gualosuchus* from the Chanares Formation of Argentina, and grouped them along with *Proterochampsa* and *Cerritosaurus* in the single family Proterochampsidae of the suborder Proterosuchia. Although the Proterochampsidae show many parasuchian affinities, the absence of the postfrontal bone in these forms raises a serious problem, as this bone is ubiquitous in all parasuchids. Moreover, the pineal foramen, being present in primitive species, such as *Paleorhinus* (= *Parasuchus*) *scurriensis*, ought to be present in the ancestral form. This is also lacking in the Proterochampsidae. Furthermore, the post-cranial skeleton of the Proterochampsidae does not show any positive relationship to that of parasuchids (Romer 1972). However, one important feature seen in these forms is the initiation of the movement of the external nares, as slit-like structures, well back on to the dorsal surface. This suggests that the parasuchians could be the direct descendants of the Proterosuchia by the process of moving the external nares back along the skull in a longirostral lineage. The Proterochampsidae must be regarded as an aberrant offshoot of the primitive proterosuchian stock (Romer 1971, 1972).

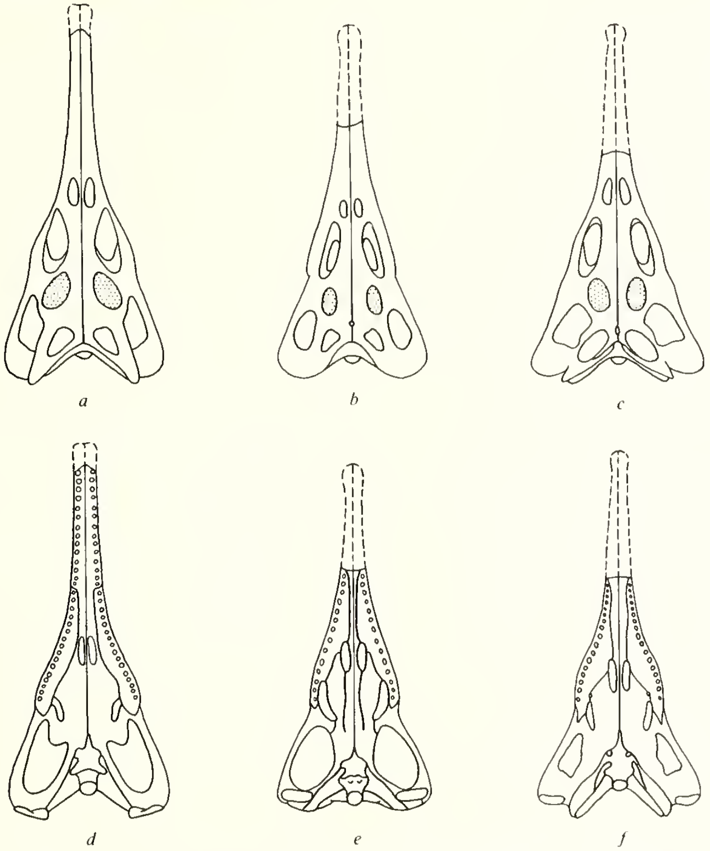
The skull of *Proterosuchus* shows some parasuchian traits (Gregory 1962). The general form of the skull (Cruickshank 1972) is elongate, with downturned premaxillae, indicating a tendency toward lengthening of the snout. It also possesses a postfrontal bone and a pineal foramen. But the gap between *Proterosuchus* and a typical parasuchian is so great as to make an assumption of relationship little more than an interesting possibility.

Jaekel (1910) described *Mesorhinus fraasi* as a primitive parasuchian from the Early Triassic Buntsandstein of Germany. Gregory (1962) doubted its parasuchian affinity, as the figured specimen lacks the characteristic long rostrum and is recorded too early. He also doubted that the horizon of *Mesorhinus* had been correctly attributed. Nevertheless, the preserved part of the skull of *Mesorhinus* exhibits almost all of the archaic features of parasuchians listed by Gregory, i.e.

low occiput;
post-temporal arcade at the level of the skull roof;
external nares well in front of the antorbital fenestrae;
squamosal without posterior hook;
large post-palatine fenestra;
large interpterygoid vacuity;
retention of the pineal foramen.

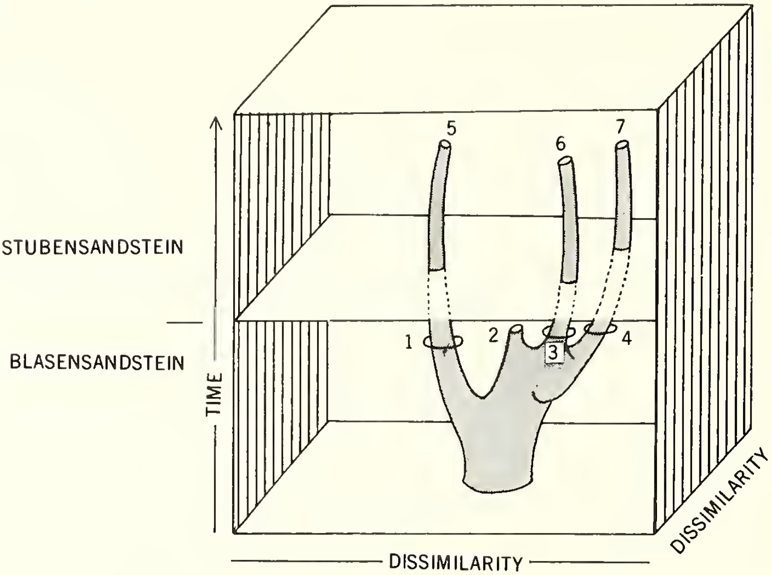
The close similarity of the skull *Mesorhinus* to those of primitive parasuchians such as *Paleorhinus* (= *Parasuchus*) *scurriensis* is very striking (text-fig. 17). There seems ample evidence for regarding *Mesorhinus* as a very primitive parasuchid. If *Mesorhinus* is truly a parasuchid and if it comes from the Early Triassic, it is by far the earliest member of the family. Unfortunately the only specimen of *Mesorhinus* was destroyed during the war in 1945 (Dr. Frank Westphal, pers. comm.), and further re-examination is therefore impossible. Future discovery of good material of *Mesorhinus* may help to solve this long-standing problem regarding the origin of parasuchians.

There seems to be two distinct phyletic lines in the parasuchian evolution, one containing *Francosuchus* and *Mystriosuchus*, the other containing *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon*. *Mystriosuchus* is obviously an advanced genus, similar to *Nicrosaurus* and *Rutiodon* in its high occiput, depressed post-temporal arcade, and posterior external nares. It resembles *Francosuchus* in the absence of squamosal process, in retaining homodont dentition, and sharing characteristic long and slender rostrum. The similarity of high rostral ratio is suggestive of phyletic relationship between them. This trend towards a more elongate rostrum suggests that *Francosuchus* has diverged from the primitive stock (?*Mesorhinus*) in a separate phyletic line from the rest of the genera earlier than the Early Triassic, leading to *Mystriosuchus*. Furthermore, both *Francosuchus* and *Mystriosuchus* occur only in Germany, which supports this hypothesis. The subfamily Mystriosuchinae (*nom. transl. ex* Mystriosuchidae von Huene 1915) is proposed herein to include *Francosuchus* and *Mystriosuchus*.



TEXT-FIG. 17. A comparison of the skull in *Mesorhinus*, *Paleorhinus*, and *Parasuchus*. *a*, *d*, dorsal and ventral views of *Parasuchus hislopi* Lyd. (specimen ISI R 44); *b*, *e*, dorsal and ventral views of *Mesorhinus fraasi* (after Jaekel 1910); *c*, *f*, dorsal and ventral views of *Paleorhinus scurriensis* (after Langston 1949). In this figure the skulls have been reduced to a unit length in order to facilitate comparisons of proportions.

In the rest of the genera, the progressive evolution in another phyletic line can be seen. Gregory (1962) has pointed out that *Paleorhinus*, though approaching closely the structural ancestry for the parasuchians, must be regarded as slightly off the direct line of development that led to the more highly specialized genera, as this subgenus occurs in the same horizons as *Angistorhinus* and *Rutiodon*. The different subgenera of *Parasuchus* may represent the beginning of a divergence which led eventually to the later generic lines. The derivation of *Rutiodon* from the intermediate form *Angistorhinus* is rather straightforward, by the depression of the supratemporal fenestra and subsequent hooking of the squamosal. The presence of overlapping scutes in *Nicrosaurus* indicates an early separation from *Angistorhinus–Rutiodon* lineage. *Parasuchus*, however, develops overlapping scutes. Thus *Nicrosaurus* might have descended from a *Parasuchus*-like ancestor and acquired its similarities to *Rutiodon* independently. *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon* are grouped here into another subfamily Parasuchinae (*nom. transl. ex* Parasuchidae Lydekker, 1885). The inferred phylogenetic relationships may be represented by the following diagram (text-fig. 18).



TEXT-FIG. 18. Three-dimensional representation of the phylogeny of the parasuchians. 1, *Francosuchus*; 2, *Paleorhinus* (= *Parasuchus*); 3, *Parasuchus*; 4, *Angistorhinus*; 5, *Mystriosuchus*; 6, *Nicrosaurus*; 7, *Rutiodon.*

The extinction of the parasuchians, like their sudden emergence, is a baffling phenomenon to comprehend. They disappeared suddenly at the close of the Triassic at a time coinciding with the first wave of reptilian extinction, and were replaced by the crocodilians. The parasuchians were excellently adapted for a predatory life in amphibious habitat, having little to fear from their enemies. Their extinction is not a case of competitive exclusion. Yet they disappeared, leaving no descendants, and after their disappearance, the crocodilians, hitherto small reptiles, grew large and occupied successfully the similar ecological niche. Why should the parasuchians have failed to survive beyond the Triassic, while their contemporaries, the crocodilians, still survive? The question remains unanswered.

AGE AND THE CORRELATION OF THE MALERI FORMATION

The Maleri sediments are continental clastics of the Gondwana Group, highly variable in coarseness, grain size, and composition both along and across the strike of the formation. Three main lithological units are encountered: these are thick, unlithified red clays, fine-grained white sandstones, and pale-green lime-pellet rocks. The sediments are interpreted as fluviatile channel, interchannel, and back-swamp deposits (Sengupta 1966; Kutty 1971).

The flora is poorly documented in the Maleri sediments. The known fauna consists mostly of vertebrates, which are varied and well represented. The only invertebrate member so far discovered is the freshwater unionid. The occurrence of *Parasuchus* in the Maleri Formation is of particular significance as it may bear upon the age and the correlation of the sediments.

The Maleri vertebrates consist of three kinds of fishes, of a single amphibian genus, and of various reptiles. A complete list of the Maleri vertebrates, known to date, is given below (Table 4).

TABLE 4

Faunal list	Stratigraphic affinities
Fishes	
Dipnoi—*Ceratodus hunterianus*	Mesozoic
Subholostei—unnamed genus and species	
Pleuracanths—teeth resembling *Pleuracanthus parvidens*	Triassic
Amphibian	
Metoposaurs—*Metoposaurus maleriensis*	Late Triassic (Carnian through Middle Norian)
Reptiles	
Rhynchosaurs—*Paradapedon huxleyi*	Late Triassic (Carnian through Middle Norian)
Parasuchians—*Parasuchus hislopi*	Late Triassic (Late Carnian to Early Norian)
Aetosaurs—scutes similar to *Typothorax*	Late Triassic
Thecodontosaurs—unnamed genus and species	Late Triassic
Traversodonts—similar to *Exaeretodon*	Late Triassic
Coelurosaurs—similar to *Coelophysis*	Late Triassic

The better-known faunal elements in the above list are the amphibian *Metoposaurus* (Roy Chowdhury 1965), the rhynchosaur *Paradapedon* (Chatterjee 1974), and the parasuchian *Parasuchus*. The travesodont is very similar to *Exaeretodon* of the Ischigualasto Formation of South America. The lungfish *Ceratodus* is represented by isolated teeth, including vomerine teeth (Jain 1968), and has a long geological history. The rest of the fauna is insufficiently known at present, and as such its stratigraphic importance cannot be ascertained.

There has been a good deal of discussion in the past concerning the age of the Maleri Formation. Earlier workers tended to regard both the Maleri and the overlying Kota Formations as Liassic. Von Huene (1940) and Colbert (1958) suggested a Late Triassic age for the Formation, as the parasuchians and the metoposaurs are confined to the Late Triassic sequences of North America and Germany. Roy Chowdhury (1965) has shown that the Maleri metoposaur, *Metoposaurus maleriensis* is extremely similar to that of North America and Germany, the differences being on a specific level. In Germany the metoposaurs range in age from horizons equivalent to Schilfsandstein up to Blasensandstein. In North America they have a longer geological history and extend up to horizons equivalent to the Stubensandstein of Germany, but they show no stratigraphically useful varieties (Colbert and Imbrie 1956). On the evidence of the metoposaurs, Roy Chowdhury thus postulated a Carnian through Middle Norian age for the Maleri Formation.

Rhynchosaurs are fairly well distributed throughout the Trias. Chatterjee (1969) grouped the known rhynchosaur genera, on the basis of their morphologic characters, into three well-defined subfamilies representing three stages in rhynchosaur evolution, considered characteristic of the Early, Middle, and Late Triassic, respectively. The Maleri genus *Paradapedon* is included in the advanced subfamily Hyperodapedontinae, along with *Hyperodapedon* and *Scaphonyx*, and the Maleri Formation is equated with the Lossiemouth Beds of Scotland as well as with the Santa Maria and Ischigualasto Formations of South America.

The parasuchians, however, offer a more accurate dating of the Maleri Formation than do the metoposaurs and rhynchosaurs. Gregory (1956, 1962, and 1969) has attempted a palaeontological subdivision of the Carnian to Middle Norian faunas of North America and Germany on the basis of the parasuchians, as their skulls were undergoing rapid structural modifications through a limited geological time range. In Germany the primitive genus *Francosuchus* occurs in the Blasensandstein of the Middle Keuper, whereas the advanced genera such as *Mystriosuchus*, *Rutiodon*, and *Nicrosaurus* are common higher up in the Stubensandstein. A similar situation is observed in North America also. Here the primitive and intermediate genera such as *Parasuchus* (*Paleorhinus*) and *Angistorhinus* are restricted to beds probably equivalent to the Blasensandstein of Germany, whereas the advanced genera like *Rutiodon* and *Nicrosaurus* are abundant in horizons equivalent to the Stubensandstein. The primitive and advanced genera do not occur in the same stratum, except in Crosby County, Texas, where a primitive species of *Rutiodon* is found along with *Parasuchus* (*Paleorhinus*). The primitive and advanced genera represent successive stages in parasuchian evolution and occur in progressively younger deposits.

As the geological range of primitive parasuchians such as *Parasuchus* in North America and *Francosuchus* in Germany is known from Gregory's work, the upper limit of the Maleri and Tiki Formations can be fixed as Early Norian, equivalent to the Blasensandstein of Germany. The lower limit may extend down to the Schilfsandstein, as a doubtful record of a parasuchian jaw is known from this horizon (Gregory 1969). Thus the age range of the Maleri Formation is probably Late Carnian to Early Norian of the standard marine sequence, i.e. from the Schilfsandstein to the Blasensandstein of the German continental Trias. This is exactly the range of metoposaurs in Germany. A tentative correlation of the parasuchian-bearing sediments is given in the following table (adapted from Gregory 1956, 1969; Anderson and Anderson 1970).

TABLE 5. PROVENANCES OF THE PARASUCHIDAE.

	Alpine facies	W. Europe Germanic facies	United States of America Atlantic coast (Nova Scotia-N. Carolina) Newark group	United States of America Texas + E. New Mexico Dockum group	United States of America Arizona (Colorado Plateau)	United States of America Wyoming	India Pranhita-Godavari Valley	India Son-Mahanadi Valley	W. China (Shansi & Sinkiang)	North Africa (Morocco)
LATE TRIASSIC	RHAETIAN	Rhaetian*? (gen. indet.)					Dharmaram Formation		Lufeng* Series (gen. indet.)	
	NORIAN	Knollenmergel	Brunswick Fm.* upper part (*N.*) Portland Arkose Meriden Fm.	Redonda Fm.* (undescribed)	Wingate Fm.*? Moenave Fm. Owl Rock M. (gen. indet.)					
		Stubensandstein* (*N.*, *M.*, *R.*)	New Haven Arkose* (*N.*) Brunswick Fm. lower part Lockatong Fm.* (*N.*) Cumnock Fm.* (*R.*) Stockton Fm.* (*N.*)	Upper fauna* (*N.*) Middle fauna* (Tecovas Shale) (*N.*)	CHINLE FORMATION Upper fauna* (*N.*) Lower fauna* (*R.*, *N.*) Shinarump M.* (unnamed)					Morocco fauna* (undescribed, similar to *M.*)
	CARNIAN	Blasensandstein* + Lehrbergstufe (*F.*)		Basal fauna* (*P.*, *A.*)		Popo Agie M.* (Chugwater Fm.) (*P.*, *A.*)	Maleri Fm.* (*PS.*)	Tiki Fm.* (*PS.*)		
		Schilfsandstein*? (gen. indet.)								
		Lettenkohle								

* Parasuchid-bearing horizon

Abbreviations: *A.* = *Angistorhinus*; *F.* = *Francosuchus*; *M.* = *Mystriosuchus*; *N.* = *Nicrosaurus*; *P.* = *Paleorhinus*; *PS.* = *Parasuchus*; *R.* = *Rutiodon*

TABLE 5. PROVENANCES OF THE PARASUCHIDAE.

	Alpine facies	W. Europe	United States of America				India		W. China (Shansi & Sinkiang)	North Africa (Morocco)
		Germanic facies	Atlantic coast (Nova Scotia-N. Carolina) Newark group	Texas + E. New Mexico Dockum group	Arizona (Colorado Plateau)	Wyoming	Pranhita-Godavari Valley	Son-Mahanadi Valley		
LATE TRIASSIC	RHAETIAN	Rhaetian*? (gen. indet.)					Dharmaram Formation		Lufeng* Series (gen. indet.)	
	NORIAN	Knollenmergel	Brunswick Fm* upper part (*N.*) Portland Arkose Meriden Fm.	Redonda Fm* (undescribed)	Wingate Fm.*? Moenave Fm. Owl Rock M. (gen. indet.)					
		Stubensandstein* (*N.*, *M.*, *R.*)	New Haven Arkose* (*N.*) Brunswick Fm lower part Lockatong Fm.* (*N.*) Cumnock Fm* (*R.*) Stockton Fm* (*N.*)	Upper fauna* (*N.*) Middle fauna* (Tecovas Shale) (*N.*)	CHINLE FORMATION Upper fauna* (*N.*) Lower fauna* (*R.*, *N.*) Shinarump M.* (unnamed)					Morocco fauna* (undescribed, similar to *M.*)
	CARNIAN	Blasensandstein* + Lehrbergstufe (*F.*)		Basal fauna* (*P.*, *A.*)		Popo Agie M.* (Chugwater Fm.) (*P.*, *A.*)	Maleri Fm.* (*PS.*)	Tiki Fm* (*PS.*)		
		Schilfsandstein*? (gen. indet.)								
		Lettenkohle								

* Parasuchid-bearing horizon

Abbreviations: *A* = *Angistorhinus*; *F.* = *Francosuchus*; *M* = *Mystriosuchus*; *N.* = *Nicrosaurus*; *P.* = *Paleorhinus*; *PS* = *Parasuchus*; *R.* = *Rutiodon*

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THE JAW APPARATUS OF RECENT *NAUTILUS* AND ITS PALAEONTOLOGICAL IMPLICATIONS

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ABSTRACT. The jaw apparatus of extant cephalopods consists of articulated beak-like mandibles which are composed of chitin and powered by strong buccal muscles. Upper and lower jaws of *Nautilus* possess conspicuous calcite coverings; the upper jaw is characterized by a robust, arrow-shaped calcite element, the rhyncholite; the anterior region of the lower jaw possesses a delicately denticulated calcite element, the conchorhynch. The rhyncholite functions as an incisor operating against the lower cutting edge of the conchorhynch, producing a powerful shearing action. Rhyncholites extracted from the extant species *Nautilus pompilius*, *N. macromphalus*, and *N.* cf. *pompilius* are indistinguishable, in contrast to the conchorhynchs, which are species-distinctive. Both rhyncholites and conchorhynchs range from Middle Triassic to Recent. Circumstantial evidence, including the geologic range, the analogy of *Nautilus*, and the contrasting form of ammonoid and dibranchiate mandibles, indicates that rhyncholites and conchorhynchs belong exclusively to the Nautilaceae. In view of the close similarity between fossil and modern cephalopod jaws, the use of parataxial form genera such as *Rhyncolites* Biguet, 1819 and *Conchorhynchus* de Blainville, 1827 is both practical and necessary for classifying isolated cephalopod jaw elements.

NAUTILUS, the only surviving tetrabranchiate cephalopod, is distinguished from modern dibranchiates by such features as the chambered external shell, the number of gills, and the less complex eye and statocyst. Additionally, *Nautilus* is the only extant cephalopod which secretes calcareous jaw elements (text-fig. 1); the mandibles of octopods, sepiids, and teuthids are composed entirely of chitin and they characteristically have sharper, more saggitate, beaks (text-fig. 2).

Fossil remains of cephalopod jaws, although generally rare, are geographically widespread and well known in rocks of Mesozoic and Cenozoic age. Most commonly encountered as fossils are the isolated, calcified portions of the upper jaw (rhyncholites) and less frequently, the lower jaw (conchorhynchs); the noncalcified chitinous portions of the jaws are very rarely preserved. Rhyncholites and conchorhynchs have been known in the palaeontological literature for over 150 years. Some early authors mistakenly identified them as avian beaks (*fide* d'Orbigny 1825) and cirripeds (von Schlotheim 1820), but their general similarity to modern squid and sepiid mandibles was recognized by Gaillardot (1824) and they were thought to belong to belemnoids by Biguet (1819), de Blainville (1827), and others. Although d'Orbigny (1825) thought they belonged to *Nautilus*, it was not until Sir Richard Owen's memoir on *Nautilus* was published in 1832 that the exact affinity with shelled cephalopods was demonstrated. Additional descriptions of *Nautilus* mandibles have been presented by Foord (1891), Griffin (1900), Willey (1902), Teichert *et al.* (1964), and most recently by Gasiorowski (1973). In spite of the seemingly well-documented status of *Nautilus* mandibles and their fossil counterparts, confusion has persisted regarding the morphology, terminology, and palaeontological implications of the various

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elements. The present study is an attempt to clarify these matters, in addition to presenting new data and interpretations.

MATERIAL

We have been fortunate in having had considerable comparative material available for study, including the following:

Nautilus pompilius Linné, 1758 (SUI 42422–42433); ten dried mandibles from Tinaogan Reef, north of Bindoy, Tañon Straits, Negros, Philippines (N. Haven 1971).

Nautilus pompilius Linné, 1758 (DMNH 106740); alcohol-preserved animal from 200 m depth off Medina Point, Gingoog Bay, Mindanao, Philippines (H. K. Dugdale and B. Abrea Jan. 1975).

Nautilus macromphalus Sowerby, 1849 (SUI 42434); two formalin-preserved buccal masses, New Caledonia (A. Bidder).

Nautilus macromphalus Sowerby, 1849 (SUI 35924); formalin-preserved animal, from Baie du Sandal, Lifou, Loyalty Islands ('animal F' of Denton and Gilpin-Brown 1966, p. 729).

Nautilus macromphalus Sowerby, 1849 (SUI 42163, 42164); two alcohol-preserved animals, Nouméa, New Caledonia (Mme. Catala-Stucki, R. A. Davis 1975).

Nautilus cf. *pompilius* Linné, 1758 (SUI 42435–42441); eight alcohol-preserved buccal masses, from 155 m depth off Mutremdiu Point, Uchelbeluu Reef, Belau (Palau) Islands, W. Caroline Islands (D. Faulkner 1976).

For the benefit of future workers, it should be noted that alcohol should be used to preserve the buccal mass instead of formalin, for in all of the formalin-preserved specimens studied, the calcified portions of the mandibles had been partially to completely dissolved.

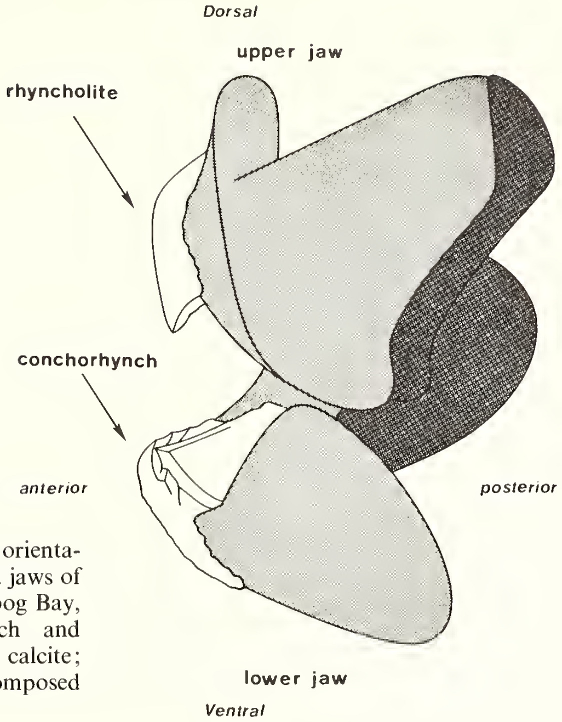
Materials utilized are reposited at the following institutions (with abbreviations as cited in text): British Museum (Natural History) BMNH; Delaware Museum of Natural History (DMNH); University of Iowa, Department of Geology (SUI).

THE JAW APPARATUS OF *NAUTILUS*

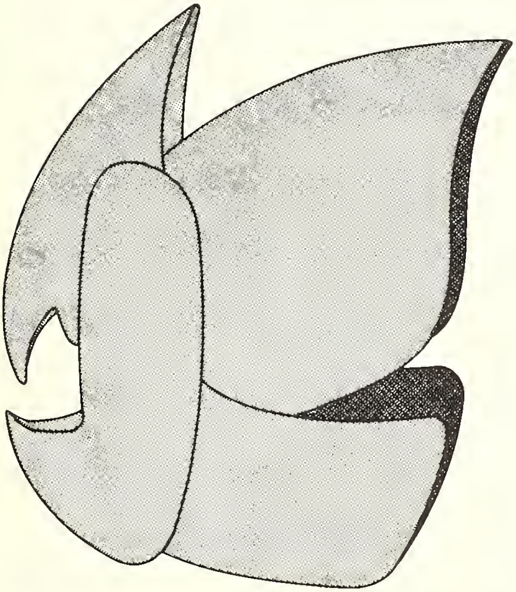
Morphology

The buccal mass of *Nautilus* is covered by a thin, muscular membrane which coalesces with the oesophagus aborally and terminates orally in circlets of buccal papillae surrounding the mouth (Pl. 9, fig. 9). The space within the buccal mass is occupied by more than a dozen separate muscles and by a prominent tongue, which partly bears the large radula. Four fleshy folds, the anterior and posterior prelingual processes of Griffin (1900), project in front and on either side of the anterior portion of the tongue; two additional projections located on both sides of the posterior portion of the tongue bear salivary gland pores.

The jaws, which are enclosed by the buccal membrane, are strong and flexible during life, but rapidly dessicate and become brittle if exposed to air. As in other extant cephalopods, the jaws are composed of chitin. The oral, or biting surface of each jaw is dense and hard, in contrast to the flanks, which are quite flexible. However, infra-red absorption spectra (text-fig. 3) show no compositional differences between different parts of the chitinous jaw. The upper jaw is enclosed within the larger lower jaw (Pl. 9, figs. 7, 8). Each jaw is folded, and thus double-walled, anteriorly. The outer surfaces of both jaws (i.e. those portions in contact with the buccal membrane)



TEXT-FIG. 1. *Nautilus* mandible terminology and orientation. Oblique lateral view based on disarticulated jaws of *Nautilus pompilius* (DMNH 106740) from Gingoog Bay, Mindanao, Philippines (×1·5). Conchorhynch and rhyncholite (both in white) are composed of calcite; the other portions of the mandibles (stippled) are composed of chitin.



TEXT-FIG. 2. Typical dibranchiate mandibles, represented by Recent *Loligo* sp. (×5). Mandibles are composed entirely of chitin. Terminology and orientation as in text-fig. 1, except drawn in articulated position.

are covered with distinctive, closely spaced, concentric ornament, interpreted as growth lines. On the flanks of the lower mandibles these growth lines are transected by delicate, irregularly spaced radial ridges (Pl. 9, figs. 4, 10).

Calcification is restricted to the anterior portion of both mandibles (text-fig. 4). The calcified portion of the lower jaw, the conchorhynch, comprises three distinct areas: (*a*) irregular deposits of calcite on the outer surface (Pl. 9, figs. 3, 14) that are continuous with (*b*) a distinctively denticulated occlusal or oral surface (Pl. 9, figs. 6, 16), which in turn extends ventrally to form (*c*) a smooth calcareous layer on the inner anterior portion of the lower jaw (Pl. 9, fig. 5). In *N. pompilius*, the oral or occlusal surface displays a strong, T-shaped ridge, or denticle, at the apex of the mandible, with three progressively smaller parallel denticles along the outer flanks. Adjacent to these denticles a furrow extends along the full length of the occlusal surface. The inner margin of the furrow is a sharply defined ridge, which serves as a shearing or cutting edge (Pl. 9, figs. 5, 6). In contrast to *N. pompilius*, the conchorhynch of *N. macromphalus* displays a series of four highly crenulated ridges posterior to the tightly crenulated, T-shaped apical ridge. Although these denticles stand out in sharp relief, they show no evidence of breakage or wear even in large, presumably mature specimens (Pl. 9, figs. 10, 11, 15, 16). Conchorhynchs of *N.* cf. *pompilius* available to us for study are all badly worn and details are not readily distinguishable, but they are similar to those of *N. macromphalus*, in having four relatively sharp, steep denticles. The inner surface of the *Nautilus* conchorhynch varies in detail from specimen to specimen; it is generally smooth, but some display shallow, irregularly spaced dorsoventral furrows. Removal of the conchorhynch from the lower jaw exposes the anterior surface, which in both *N. pompilius* and *N. macromphalus* is distinguished by a broad median ridge tapering towards the occlusal surface; subsidiary, irregularly spaced ridges may be present on the surface of the median ridge (Pl. 10, fig. 17). In neither *N. pompilius* nor *N. macromphalus* is the distinctive chevron pattern of biserial grooves on each side of the median ridge present as in *N.* cf. *pompilius* (Pl. 10, fig. 16). This feature is characteristic of many fossil forms, including the type species *Conchorhynchus avirostris* von Schlotheim, 1820 (Pl. 10, fig. 8); see also Gaillardot's (1824) specimens (in Teichert *et al.* 1964, fig. 338, 1*c*, *f*).

EXPLANATION OF PLATE 9

Mandibles of *Nautilus pompilius* Linné, 1758. (1–6) and *Nautilus macromphalus* Sowerby, 1849 (9–16). All figures ×1 except 6, 16 (×3), and 15 (×2·5).

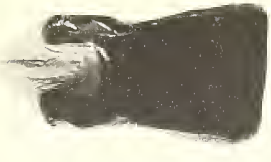
Figs. 1–6, *N. pompilius* (DMNH 106740) from Gingoog Bay, N. Mindanao, Philippines: 1, 2, ventral and lateral views showing rhyncholite *in situ*; 3–5, anterior, lateral, and dorsal views of lower mandible showing conchorhynch *in situ*; 6, enlarged dorsal view of conchorhynch.

Figs. 7, 8, lateral and anterior views of articulated mandibles of *N.* cf. *pompilius* (SUI 42440) from Mutremdiu Point, Belau (Palau) Islands.

Fig. 9, lateral view of buccal mass of *N. macromphalus* (SUI 35924) from Lifou, Loyalty Islands, showing mandibles covered by buccal membrane, buccal papillae encircling mouth and oesophagus extending from lower right of buccal mass.

Figs. 10–16, *N. macromphalus* (SUI 42163) from Nouméa, New Caledonia: 10, 11, 14, lateral, dorsal, and anterior views of lower mandible with conchorhynch *in situ*; 15, 16, enlarged lateral and dorsal views of conchorhynch; 12, 13, ventral and lateral views of upper mandible showing rhyncholite *in situ*.

PLATE 9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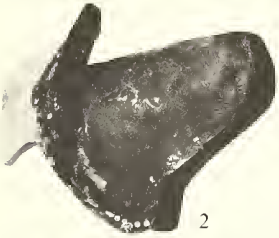
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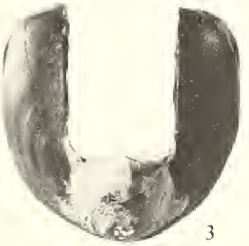
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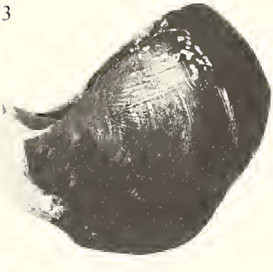
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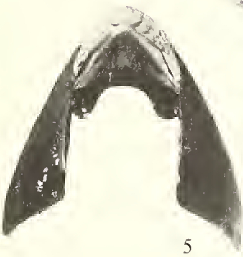
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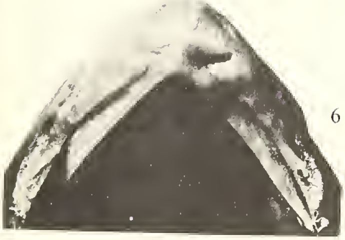
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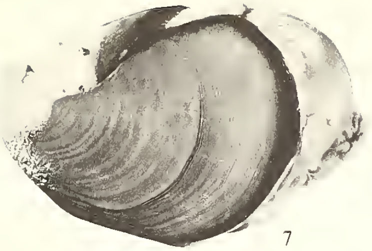
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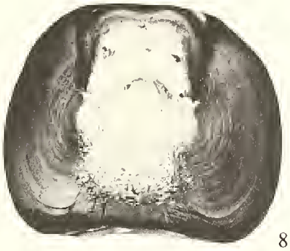
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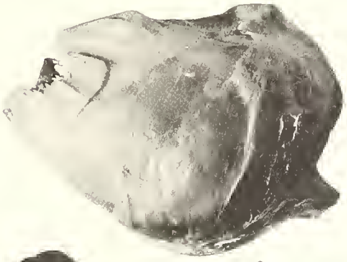
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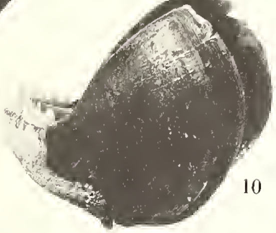
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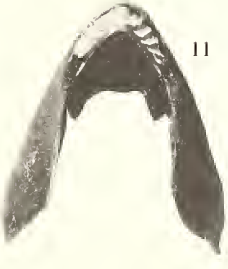
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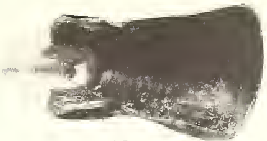
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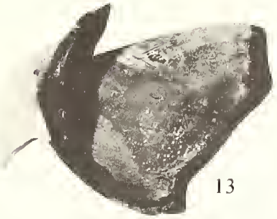
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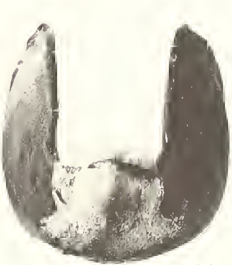
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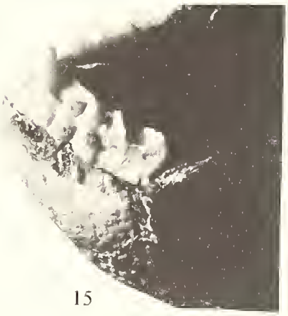
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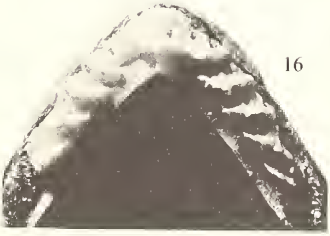
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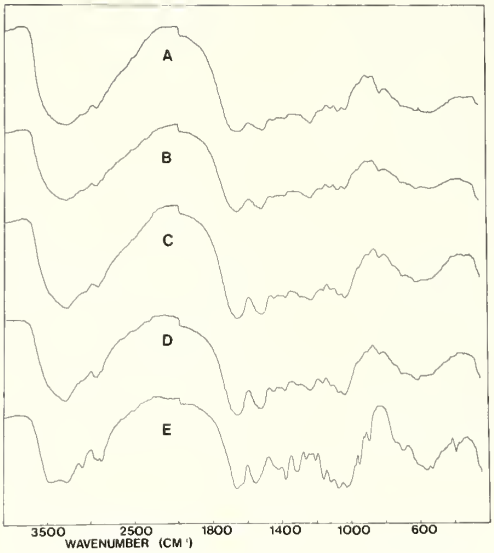
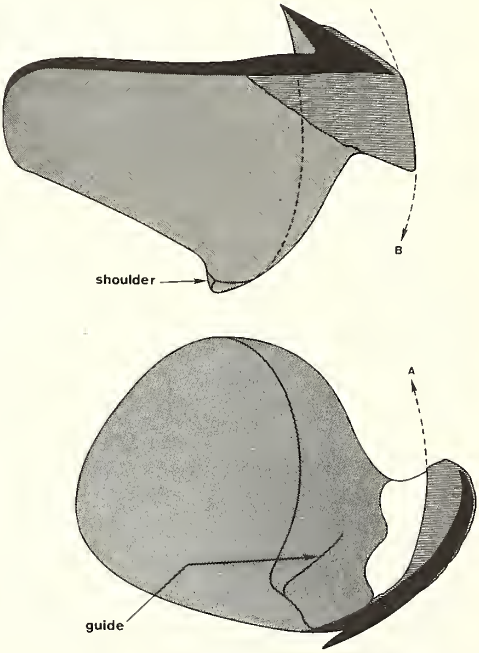
SAUNDERS *et al*, *Nautilus* jaw apparatus



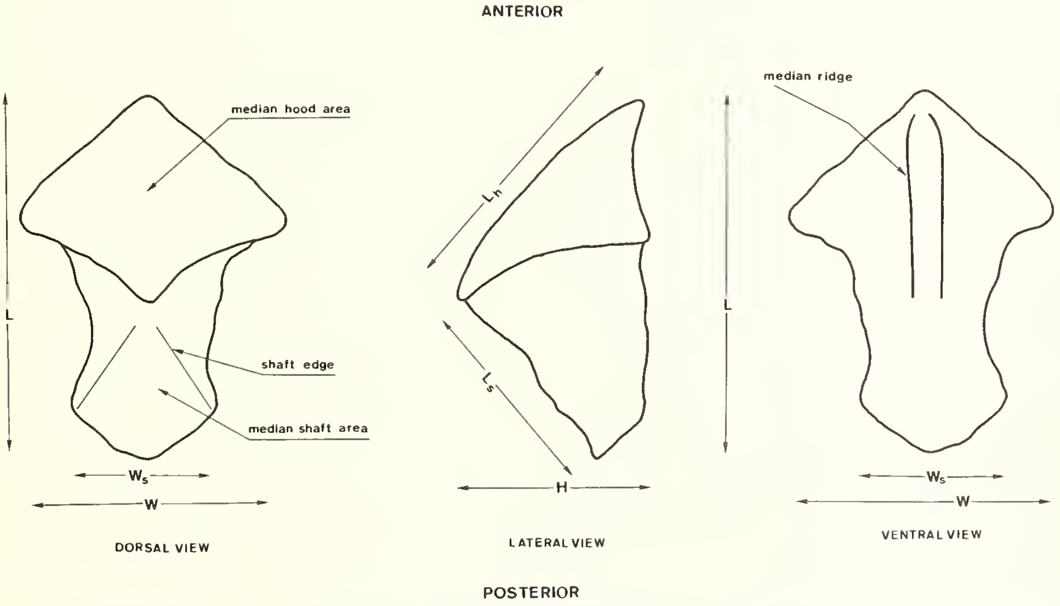
TEXT-FIG. 3. Infra-red absorption spectra of flank (A) and occlusal surface (B) of lower mandible of *Nautilus pompilius* and of occlusal surface (C) and flank (D) of lower mandible of *Loligo* sp., compared to (E) commercial chitin (from Matheson Coleman and Bell, lot P9013 CX688). Infra-red absorption spectra were obtained using a Perkin-Elmer Model 467 spectrophotometer, with samples ground and dispersed in solid potassium bromide pellets.



TEXT-FIG. 4. Schematic longitudinal cross sections of disarticulated upper and lower mandibles of *Nautilus pompilius* (× 1·75). Stippled areas represent unsectioned chitinous jaw and black represents sectioned portion of the same. White represents unsectioned calcareous conchorhynch; horizontally ruled areas represent sectioned calcareous rhyncholite and conchorhynch. During articulation, upper jaw is maintained tightly enclosed within lower jaw; *shoulder* of upper jaw is supported by and moves along *guide* of lower jaw, rhyncholite axis B is moved tightly against conchorhynch axis A, generating strong shearing effect.

The rhyncholite is the arrow-shaped counterpart to the conchorhynch. As a result of numerous studies based on isolated fossil specimens (for example, Gasiorowski 1973; Dieni 1975), the morphology and terminology of rhyncholites is well established (text-fig. 5). When *in situ*, the convex side of the rhyncholite shaft is located within the folded anterior edge of the upper jaw (Pl. 9, figs. 1, 12). The prominent, triangular hood projects ventrally from the jaw and serves as the upper counterpart of the inner cutting edge of the conchorhynch (text-fig. 4). The calcitic deposits of the hood extend over the edge and partially cover the anterior surface of the upper jaw; the exposed inner surface of the rhyncholite displays a prominent median ridge flanked laterally by depressions and in many specimens the inner surface of the shaft exhibits a series of longitudinal grooves, which vary in length and spacing (Pl. 10, figs. 2–5). There is considerable intraspecific variation in rhyncholite sculpture and proportions, as well as a high degree of overlap in the morphology of rhyncholites belonging to different extant species of *Nautilus* (text-fig. 6).

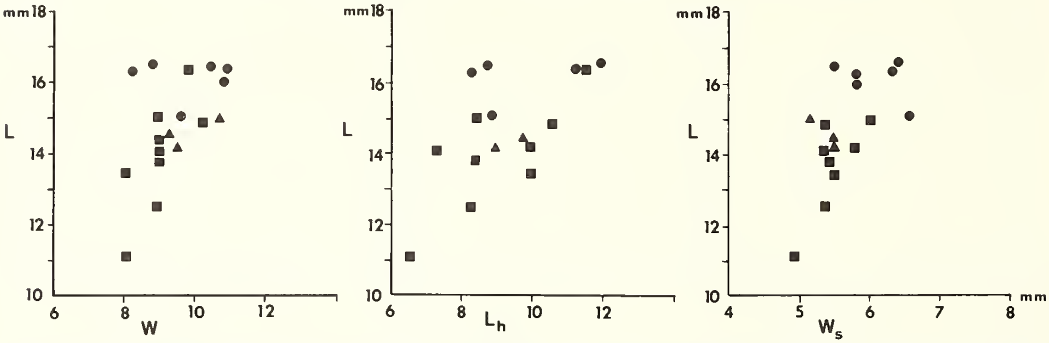
In mature specimens of *N. pompilius*, *N.* cf. *pompilius*, and *N. macromphalus*, the radula is a prominent, elongate, chitinous, ribbon approximately 10 mm wide and 30 mm long. The surface of the radula is covered by rows of 'teeth'; each row contains thirteen elements, consisting of two lateral and two median teeth and two median support plates distributed symmetrically on either side of the central tooth. The morphology of the various radula elements was well described by Griffin (1900), and the elements have been excellently illustrated by Solem and Richardson (1975). It should be noted that the radulae of these three species do not appear to be distinguishable in any respect.



TEXT-FIG. 5. Rhyncholite dimensions, terminology, and orientation. H, rhyncholite height; L, rhyncholite length; W, maximum rhyncholite width; L_h, hood length; L_s, shaft length; W_s, shaft width.

Functional morphology

Viewed as a whole, the nautiloid jaw apparatus is admirably constructed as an efficient, extremely strong device for grasping, piercing, and shearing. The mandibles are articulated so that the upper, rhyncholite-bearing jaw fits within the lower conchorhynch-bearing jaw and the sharp, triangular rhyncholite functions as an incisor, which closes smoothly against the inner cutting edge of the conchorhynch. Powered by the numerous buccal muscles, this produces an extremely strong shearing action. The prominent denticles on the outer (anterior) edge of the conchorhynch are not masticatory, since the occlusal surfaces of the upper and lower jaws are not in direct contact, but they probably aid in grasping and facilitate shearing.



TEXT-FIG. 6. Scattergram plots of rhyncholite length (L) and width (W); length (L) and length of hood (L_h); length (L) and width of shaft (W_s). Dots represent rhyncholites from *Nautilus* cf. *pompilius*, triangles represent those from *N. macromphalus*, and squares represent those from *N. pompilius*. Note high degree of intraspecific variation and overlap between species.

EXPLANATION OF PLATE 10

Fossil and Recent rhyncholites and conchorhynchs.

Figs. 1, 20, *Syrionautilus libanoticus* (Foord and Crick, 1890) (BMNH 83663) from the Upper Cretaceous, Sahil Alma, Lebanon: 1, enlarged view of rhyncholite (× 4); 20, rhyncholite in living chamber surrounded by probable remains (dark) of upper mandible (× 1).

Figs. 2–5 (inner views), 7–10 (outer views), 12–15 (lateral views), rhyncholites of *Nautilus pompilius* Linné, 1758 (SUI 42423–42426) from Tañon Strait, Negros, Philippines (× 2·5).

Figs. 6, 11, outer and inner views of *Rhyncolites hirundo* Biguet, 1819 (BMNH 83943b) from the Middle Triassic, Muschelkalk, Bavaria (× 2).

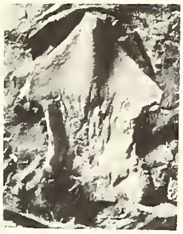
Fig. 16, posterior view of lower mandible of *N.* cf. *pompilius* Linné, 1758 (SUI 42441) from Mutremdiu Point, Belau (Palau) Islands, with conchorhynch removed showing chevron pattern of biserial grooves on anterior conchorhynch surface (× 2·5).

Fig. 17 (SUI 42432), view of lower mandible of *N. pompilius* from same locality as previous with conchorhynch removed (× 1·5).

Figs. 18, 21, anterior and dorsal views of *Conchorhynchus avirostris* (von Schlotheim) 1820 (BMNH 83493b) from same locality as previous (× 2).

Fig. 19, dorsal view of *N. pompilius* conchorhynch (SUI 42433) (× 2).

PLATE 10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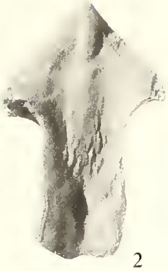
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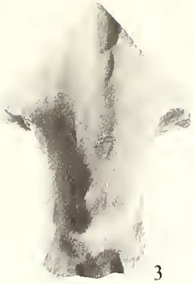
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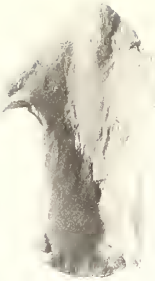
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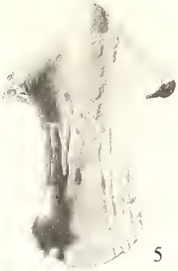
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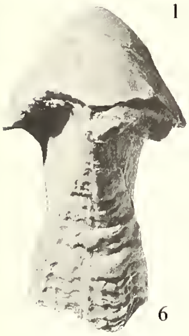
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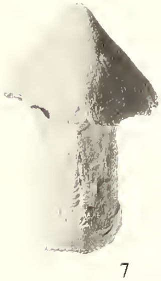
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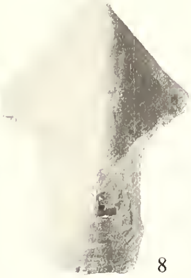
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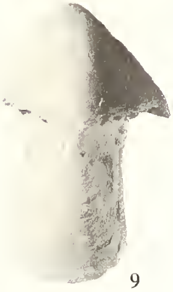
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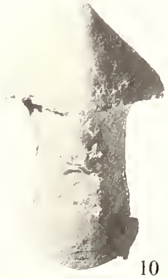
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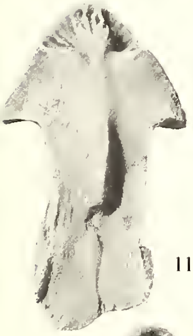
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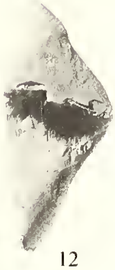
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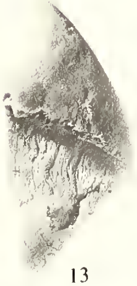
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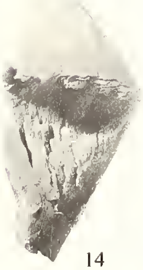
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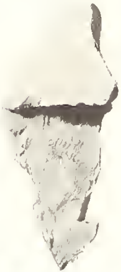
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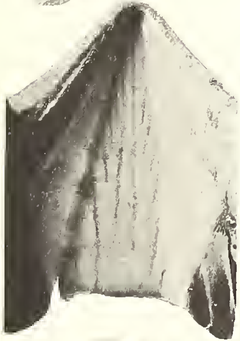
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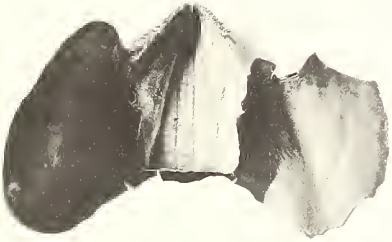
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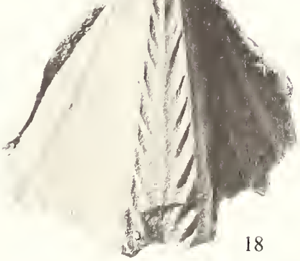
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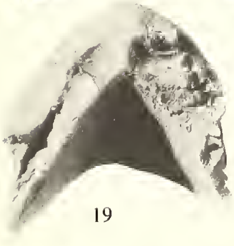
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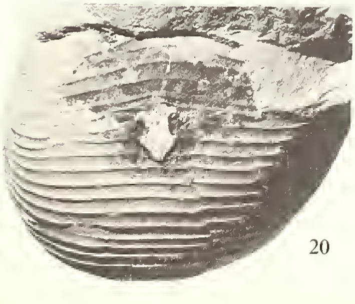
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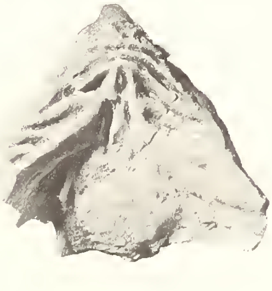
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SAUNDERS *et al.*, *Nautilus* jaw apparatus

The striking differences between the conchorhynchs of *N. pompilius*, *N. macromphalus*, and *N.* cf. *pompilius* have been described. While the functional implications of these differences are not entirely clear, a few conclusions may be made. The delicate, high-relief denticles present in the two specimens of *N. macromphalus* examined would not withstand heavy use, for example, as would be required in shell breaking and they show no evidence of wear (Pl. 9, figs. 15, 16). In contrast, most of the conchorhynchs and, to a lesser extent, the rhyncholites of *N. pompilius* and *N.* cf. *pompilius* examined show considerable wear. In several mature specimens of *N.* cf. *pompilius*, the conchorhynch has been completely worn away in places, exposing the underlying chitinous jaw, which also demonstrates conspicuous abrasions. Such signs of wear might result from a diet richer in hard or shelled foods. Unfortunately, practically no data are available regarding the actual diet of species of *Nautilus*. Observations consist primarily of comments regarding bait used in trapping *Nautilus*; various meats, including chicken (hardly natural fare, but, nevertheless an apparent favourite), fish, molluscs, and crustaceans (Griffin 1900; Dean 1901; Willey 1902; Haven 1972; D. Faulkner and P. Ward, personal communications 1976). Additionally, Griffin noted (1900, p. 159) that the crops of *N. pompilius* which he dissected (caught in chicken-baited traps) were often filled with chicken, including feathers and sheared bones. Haven (1972, p. 79) remarked that crop content consisted of bitten pieces of bait approximately 5 mm square and occasional fragments of decapod crustacean carapaces. It also appears that the jaws may be employed effectively in fighting, judging from injuries to the hood and shell which a young male *N. pompilius* suffered while caged with other males (Haven 1972, p. 79). This might be an explanation for many of the crescentic breaks commonly observed in both extant and fossil cephalopod shells.

The exact function of the nautiloid radula is not known. However, the fact that it has been retained as such a prominent structure for so long indicates its usefulness. Griffin (1900, p. 160) concluded that the radula might be used in seizing prey and as an aid in moving food into the oesophagus. This view was supported and enlarged upon by Solem and Richardson (1975). It seems that the radula could also be used in a rasping fashion against material held in place by the jaws. This might account for the finely particulate nature of food material observed in the mouth and imbedded in the radula of several of the animals dissected during the course of this study.

PALAEONTOLOGIC IMPLICATIONS

In the present paper, utilization of the term 'rhyncholite' applies only to the calcified portion of the upper mandibles found in Recent *Nautilus* and to fossil structures closely resembling them. These rhyncholites are the forms which Till (1907) referred to as '*Nautilus-Schnäbel*' and which Teichert *et al.* (1964) assigned to the genus *Rhyncolite* Biguet. This form genus was later corrected to *Rhyncolites* by Ward and Cooper (1972), by Teichert and Stanley (1975), and by Dieni (1975). The calcified elements which develop on the lower mandibles of *Nautilus* are herein referred to as conchorhynchs. Fossil conchorhynchs have been placed in the form genus *Conchorhynchus* de Blainville (Teichert *et al.* 1964). The vernacular term 'rhyncholites' has also been applied in a general sense to a large variety of fossil forms which bear no close taxonomic relationship to *Rhyncholites* or *Conchorhynchus* and which were grouped as '*Nicht-Nautilus-Schnäbel*' by Till (1907). These latter forms are not being considered here.

The general morphology of rhyncholites (as restricted herein) has remained remarkably stable since the Middle Triassic. This is exemplified by comparison of Recent *Nautilus* rhyncholites with those of Upper Cretaceous *Syrionautilus libanoticus* and to Middle Triassic specimens generally assigned to *R. hirundo* (Pl. 10). If encountered as isolated fossil elements, these forms would certainly be regarded as congeneric. Somewhat similar conservatism is shown by conchorhynchs; modern *Nautilus* conchorhynchs show considerable variation in detail, but basically the same morphology is represented by fossils as far back as the Middle Triassic, for example, *C. avirostris* (Pl. 10, figs. 18, 21). There have been many variations in the basic rhyncholite-conchorhynch plan, exemplified by numerous fossil rhyncholite form genera, distinguished by such criteria as proportions of hood, shaft form, curvature, etc. (see Teichert *et al.* 1964; Gasiorowski 1973). The lack of change in the basic form of these nautiloid jaw elements, in contrast to the rapid evolution and diversification of the shells of post-Triassic nautiloid genera, seems an unusually clear example of mosaic evolution.

In view of the close structural similarity between the modern and fossil cephalopod jaw apparatus, there is no reason to assume major differences in the jaw function of fossil versus modern counterparts. Thus, we reject portrayals of the rhyncholite-conchorhynch apparatus as a mechanism for grinding, with the ventral surface of the rhyncholite directly opposing the dorsal (oral) surface of the conchorhynch (see Rutte 1962; Teichert *et al.* 1964, fig. 340). Such interpretations are inconsistent with the known articulation, musculature, and operation of the jaw apparatus of *Nautilus*, as well as with the jaws of modern dibranchiate cephalopods and articulated fossil jaws.

The general similarity of fossil rhyncholites to those of modern *Nautilus* focuses on a taxonomic problem cited briefly by Teichert and Stanley (1975); isolated fossil rhyncholites and conchorhynchs which are indistinguishable from jaws of modern *Nautilus* may, according to rules of nomenclature, be regarded as synonyms of *Nautilus*. This is complicated by the fact that the only known fossil rhyncholite which occurs *in situ*, that of Cretaceous *S. libanoticus* (Foord and Crick, 1890) is also indistinguishable from *Nautilus* rhyncholites (Pl. 10, figs. 1, 2), although the shell form of the fossil species is quite different (Pl. 10, fig. 20). This demonstrates the practical need for utilizing a dual system of binomial nomenclature for the cephalopod jaw apparatus. We recommend retaining the present parataxial system as it has been developed, except in cases where identity of separate parts can be clearly established, as in *Nautilus* and *Syrionautilus*.

It is extremely difficult to establish the taxonomic affinity of most fossil cephalopod jaws, since they are only rarely found either *in situ* in the living chamber or associated with identifiable conch remains. There is only one unequivocal occurrence of fossil rhyncholites *in situ*: five specimens of *S. libanoticus* (Foord and Crick, 1890) from the Upper Cretaceous of Lebanon display the rhyncholite and, in some cases, remains of the chitinous jaw in the living chamber (Pl. 10, figs. 1, 20; also Foord 1891, figs. 67, 82; Teichert *et al.* 1964, fig. 343; Kummel 1964, fig. 334–1). Numerous mandible associations have been reported in Mesozoic ammonites (for example, Lehmann 1970, 1971, 1972; Schmidt-Effing 1972; Dagys and Dagys 1975); Carboniferous goniatites with mandibles and radulae were described by Closs (1967*a*, *b*) from Uruguay, and Saunders and Spinosa (1974 and unpublished) have found Mississippian, Pennsylvanian, and Permian ammonoids with mandibles in the living chambers. It is notable that in only one of the mandible-ammonoid associations cited above (Schmidt-Effing 1972) is a calcified mandibular element (conchorhynch) represented and that the uncalcified mandibles inferred to belong to ammonoids resemble more closely mandibles of modern dibranchiates than those of *Nautilus*.

The known geologic range of rhyncholites and conchorhynchs, based on isolated elements, is Middle Triassic to Recent (see Gasiorowski 1973, for detailed discussion). They are not known from the Upper Triassic, a time of major nautiloid extinction, but they are relatively abundant and diverse in the Jurassic and the Cretaceous. Although widely distributed, they are relatively rare in post-Cretaceous strata. The rhyncholite-conchorhynch range corresponds quite closely to that of the superfamily Nautilaceae. This group includes the Nautilidae and five other families of involute, compressed forms with central or dorsal siphuncle and straight to sinuous sutures (Kummel 1964). The Nautilaceae are known from the genus *Cenoceras* in the Upper Triassic and are thought to have developed from the Syringonautilidae, which became extinct in the Late Triassic (Kummel 1953). The nautilaceans achieved wide distribution and diversity during the Middle and Late Jurassic, they were abundant during the Cretaceous and Early Tertiary, but in the Late Tertiary diminished to the present single surviving genus.

While it cannot be proven directly that rhyncholites and conchorhynchs are an exclusive nautilid feature, the circumstantial implications, including rhyncholite-conchorhynch associations, their geologic range, their analogy to extant *Nautilus*, as well as the occurrence and contrasting uncalcified forms of ammonoid jaws, seem conclusive. It is tempting to extend speculation, to consider whether jaw calcification may have been a factor in the survival of *Nautilus*, which may be characterized as a relatively slow-swimming scavenger-predator somewhat removed from competition with the highly developed, agile dibranchiates and fishes. However, such speculation requires additional knowledge regarding the ecology and mode of life of *Nautilus*.

Acknowledgements. We are deeply indebted to the following individuals for providing us with the comparative material of *Nautilus* upon which this study is based: R. Tucker Abbott, Delaware Museum of Natural History, Greenville, Delaware; B. Abrea, Medina, Mindanao, Philippines; Anna M. Bidder, The University of Cambridge, Cambridge, England; Mme. Catala-Stucki, Aquarium de Nouméa, New Caledonia; Malcome R. Clarke, National Institute of Oceanography, Surrey, England; R. A. Davis, Cincinnati Museum of Natural History, Cincinnati, Ohio; Eric J. Denton, Plymouth Laboratory, Plymouth, England; H. K. Dugdale, President, Nautilus Research Corporation, Wilmington, Delaware; Douglas Faulkner, Belau (Palau) Is., W. Caroline Is.; W. M. Furnish and Brian F. Glenister, University of Iowa, Iowa City, Iowa; Norine Haven, Hopkins Marine Station, Pacific Grove, California. Study of material at the British Museum (Natural History) was kindly facilitated by M. K. Howarth and D. Phillips. Saunders has been supported in part by a National Science Foundation Grant, BMS 75-03393 and Spinosa by a Boise State University research grant. Robert L. Harrison, Boise State University, drafted many of the text-figures.

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THE FAMILIES OF THE ORNITHISCHIAN DINOSAUR ORDER ANKYLOSAURIA

by WALTER P. COOMBS, JUN.

ABSTRACT. All reasonably complete specimens of the ornithischian suborder Ankylosauria can be allocated to one of two families, the Ankylosauridae and the Nodosauridae, which differ in many anatomical features. Evolution within these two families was very conservative, with little morphological diversity. There is no truly 'primitive' ankylosaur that is morphologically suitable as a common ancestor for both families. *Scelidosaurus*, sometimes suggested as an ancestral ankylosaur, has no features diagnostic of the Ankylosauria. The origin of ankylosaurs is unknown, but the group may have an undocumented history extending back to the earliest beginnings of the Ornithischia.

MANY family groups have been proposed to subdivide the Ankylosauria, but few of these have been widely accepted. Study of excellent undescribed ankylosaur material at the American Museum of Natural History has revealed that there are two families within the Ankylosauria: the Ankylosauridae, typified by *Ankylosaurus*, *Euoplocephalus*, and *Pinacosaurus*; and the Nodosauridae, typified by *Nodosaurus*, *Panoplosaurus*, and *Sauropelta*. These two families show profound differences in almost every part of the skeleton. Virtually all known ankylosaurs can be classified in one or other of these two families, the only exceptions being fragmentary, incomplete specimens. Presented here is a brief survey of the diagnostic features of the suborder Ankylosauria with an account of important differences between the families Ankylosauridae and Nodosauridae.

The present paper is part of an extensive research programme on ankylosaurs that includes a revision of the sixty species of ankylosaurs, a general description of cranial and postcranial anatomy, endocranial anatomy, jaw muscles, teeth and diet, forelimb and hindlimb muscles, and function. A complete list of specimens examined during the course of this research is given in Appendix A.

Abbreviations. AMNH, American Museum of Natural History, New York; BM (NH), British Museum (Natural History), London; CM, Carnegie Museum, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GSM, Geologic Museum, Institute of Geologic Sciences, London; KU, University of Kansas Museum of Paleontology, Kansas; NMC, National Museum of Canada, Ottawa; NMNH, National Museum of Natural History, Washington; PU, Princeton University; ROM, Royal Ontario Museum; SMC, Sedgwick Museum, Cambridge; YPM, Yale Peabody Museum, New Haven.

TAXONOMIC USAGE

As used in this paper, the suborder Ankylosauria (= Thyreophora, in part, and Apraedentalia) contains two families: the Ankylosauridae (= Syrmosauridae) and the Nodosauridae (= Acantholididae, Polacanthidae, Hylaeosauridae, Palaeoscincidae, Struthiosaurinae, Panoplosaurinae, and Edmontoniinae; and all variants of these family group names, e.g. Acantholinae, Nodosaurinae). The family Ankylosauridae includes the following genera: *Ankylosaurus*, *Euoplocephalus*

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(= *Dyoplosaurus*, *Scolosaurus*, and *Anodontosaurus*), *Pinacosaurus* (= *Syrmosaurus*), *Talarurus*, ?*Lametasaurus*, *Peishansaurus*, *Stegosaurides*, *Heishansaurus*, and *Sauroplites*. The family Nodosauridae includes the following genera: *Acanthopholis*, *Dysganus* (in part), *Hoplitosaurus*, *Hylaeosaurus* (= *Polacanthus* and *Polacanthoides*), *Nodosaurus* (= *Stegopelta* and *Hierosaurus*), *Palaeoscincus* (in part), *Panoplosaurus* (= *Edmontonia*) *Priconodon*, *Sauropelta*, *Silvisaurus*, and *Struthiosaurus* (? = *Crataeomus*, *Danubiosaurus*, *Leipsanosaurus*, *Pleuropeltis*, and *Rhodanosaurus*). The following genera are considered Ankylosauria, *incertae sedis: Loricosaurus*, *Brachypodosaurus*, and *Paranthodon*.

SYNOPSIS OF DIAGNOSTIC FEATURES

Skull: shape and external features

Ankylosauria in general: compared to other Ornithischia, ankylosaur skulls are relatively wide and dorsoventrally compressed (Pls. 11 and 12; text-figs. 1, 3, and 4). A posteriorly placed orbit is almost entirely surrounded by bony laminae that include a postorbital shelf separating the eye from the bulk of the mandibular musculature (Haas 1969). Some ossifications contributing to laminae enclosing the orbits are unique to ankylosaurs (Maryańska MS.). In all Ankylosauria the upper temporal fenestrae are closed by encroachment of surrounding skull elements (Maryańska 1971) and by co-ossified dermal plates (text-figs. 1, 3, and 4). Dorsal and lateral surfaces of the skull, as well as the lateral side of the mandible, are covered by co-ossified dermal plates which obscure cranial sutures in all but immature specimens (Maryańska 1971). *Panoplosaurus* has a large dermal plate over the cheek region (Pl. 12), a feature that might be common to all Ankylosauria. Ankylosaurs have a poorly developed predentary bone. There is a short retroarticular but no coronoid process on the mandible.

Ankylosauridae: ankylosaurid skulls are wide, roughly triangular in dorsal view with a broad, blunt anterior end (text-fig. 1). Maximum skull width always exceeds skull length. In most genera the posterior margin of the skull roof overhangs the occipital region so that the paroccipital processes are not visible in dorsal view. Bilateral symmetry is usually better maintained by larger dermal plates along the margins of the skull than by the numerous small ossicles over the snout (text-fig. 1). A pair of large dermal plates that are fused to the squamosals may be blunt or may form pointed, pyramidal, horn-like projections at the postero-lateral corners of the skull roof (Pl. 11; text-figs. 1, 3). A pair of ossicles above the nostrils are elongate and narrow in *Euoplocephalus* (text-fig. 3) and *Pinacosaurus*, but are large and plate-like in *Ankylosaurus* (Pl. 11; text-fig. 1). A large triangular dermal plate is fused to the jugal and quadratojugal postero-ventral to the orbit. Both the lateral temporal

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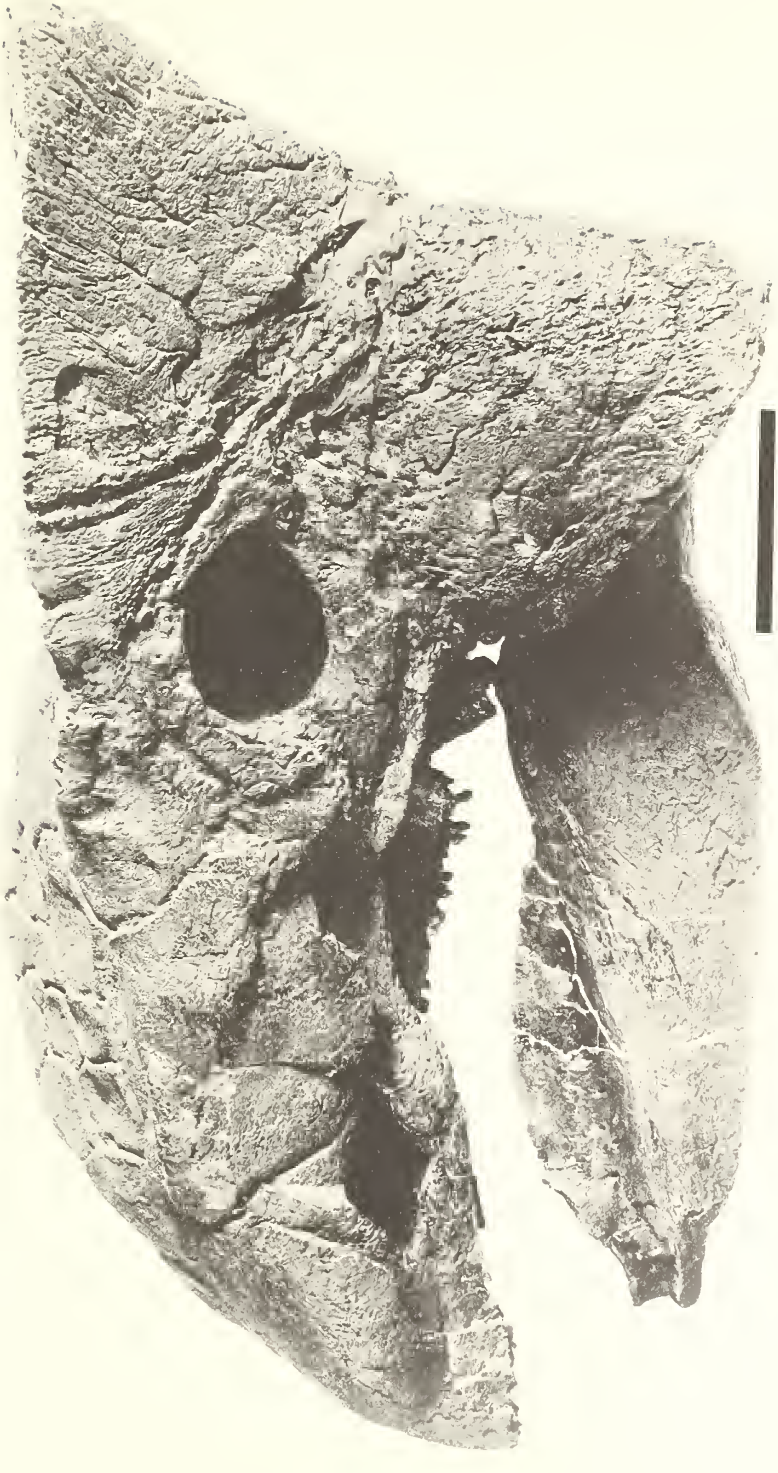
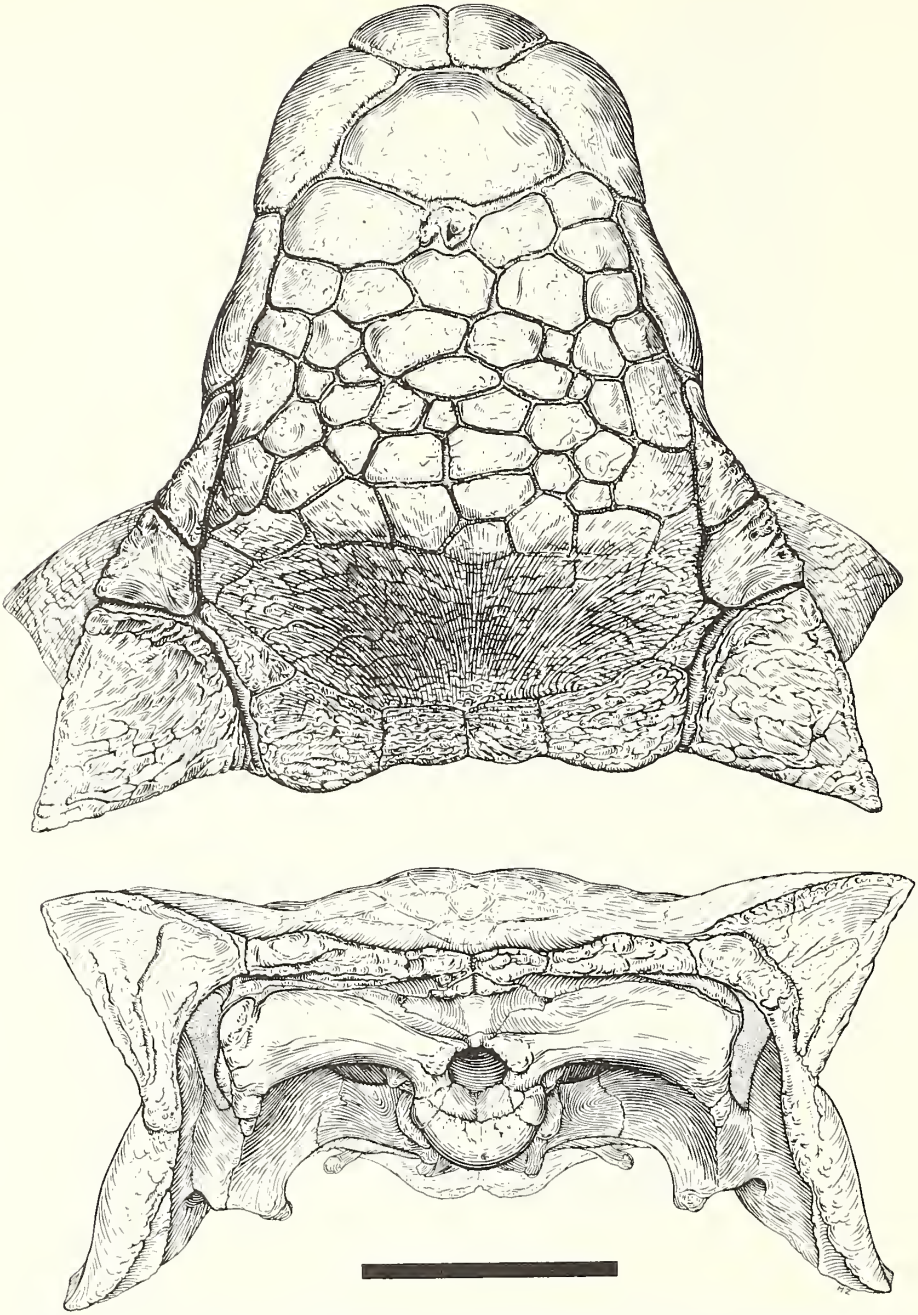
EXPLANATION OF PLATE 11

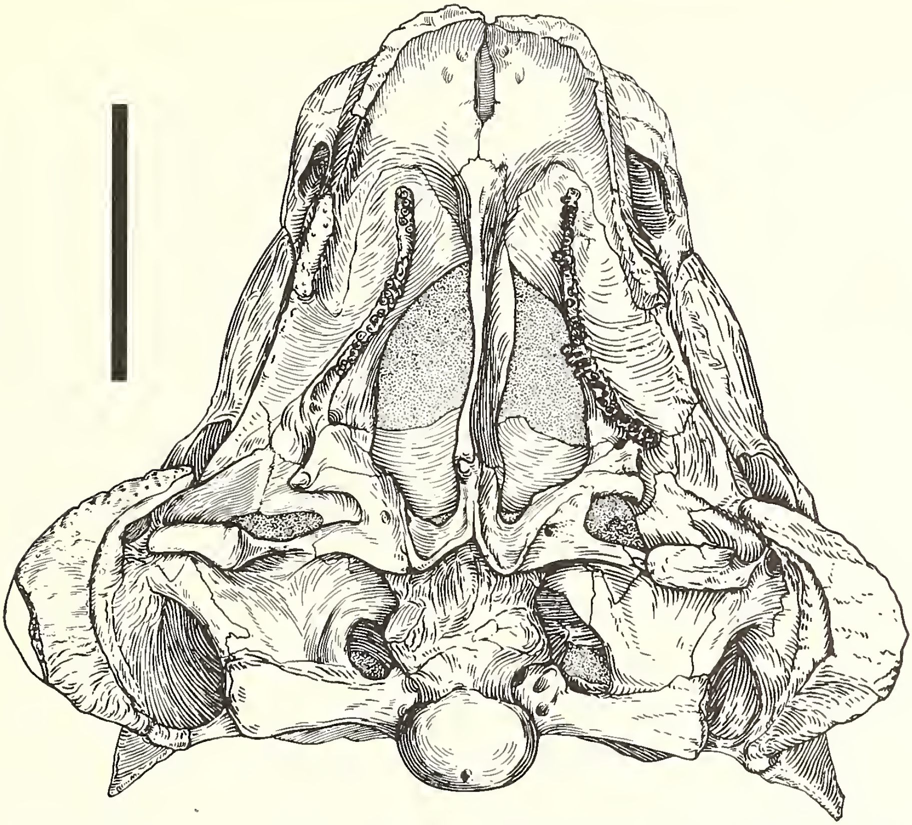
AMNH 5214, *Ankylosaurus magniventris*, skull and mandible; lateral view. Length of reference line = 10 cm.



COOMBS, ankylosaur dinosaurs



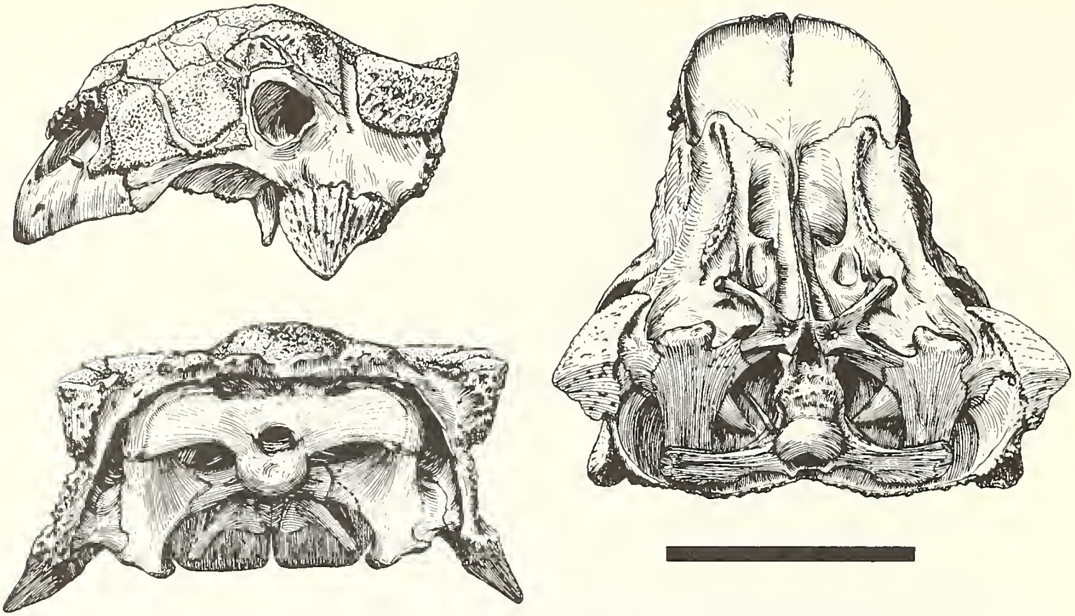
TEXT-FIG. 1. AMNH 5214, *Ankylosaurus magniventris*, skull; dorsal and posterior views. Length of reference line = 20 cm.



TEXT-FIG. 2. AMNH 5214, *Ankylosaurus magniventris*, skull; ventral view. Length of reference line = 20 cm.

fenestra and the quadrate cotylus are hidden in lateral view by this large quadratojugal plate (Pl. 11; text-fig. 3).

Nodosauridae: nodosaurid skulls are elongate and pyriform in dorsal view with a narrower, more pointed anterior end than in ankylosaurids (text-fig. 4). Skull length always exceeds maximum skull width. Posteriorly directed distal ends of the paroccipital processes project beyond the skull roof and are visible in dorsal view (text-fig. 4). Dermal plates co-ossified to the skull roof are fewer in number and relatively larger than in ankylosaurids, and bilateral symmetry is generally maintained by all cranial plates. Grooves separating these dermal plates are obscure in larger nodosaurid skulls (presumably older individuals), whereas they are deeply incised in even the largest ankylosaurid skulls. Nodosaurids have a single, trapezoidal dermal plate anteriorly between the nostrils. No pyramidal plates and consequently no horn-like projections are present at the postero-lateral corners of the skull roof. Also, there is no large triangular plate on the quadratojugal and both lateral temporal fenestra and quadrate cotylus are therefore visible in lateral view (Pl. 11). *Silvisaurus* (KU 10296) was figured with the lateral temporal fenestra hidden by a wide jugal and



TEXT-FIG. 3. AMNH 5405, *Euoplocephalus tutus*, skull; lateral, posterior, and ventral views. Length of reference line = 20 cm.

quadratojugal, but the illustration is actually an antero-lateral view (Eaton 1960, fig. 1); the lateral temporal fenestra of *Silvisaurus* is exposed in lateral view as in other Nodosauridae.

Skull: palatal, basicranial, and occipital regions

Ankylosauria in general: ankylosaurs have a flat premaxillary shelf that forms a roof over the extreme anterior end of the palate (text-figs. 2–4). In many genera there is also a bony secondary palate posteriorly between the maxillary dental rows. Maxillary teeth are withdrawn medially creating a wide maxillary shelf laterally. The maxillary dental rows are curved as seen in ventral view (text-figs. 2–4).

Ankylosauridae: ankylosaurids have broad palates with a wide, short premaxillary plate anteriorly (text-figs. 2, 3). There is no ridge connecting the cutting edge of the premaxillary beak to the anterior end of the maxillary tooth row. All known Ankylosauridae have a complex secondary palate with two horizontal shelves composed of various palatal elements (text-figs. 2, 3, and 5). Thin, antero-laterally directed mandibular rami of the pterygoids arise close to the cranial midline. In most genera the

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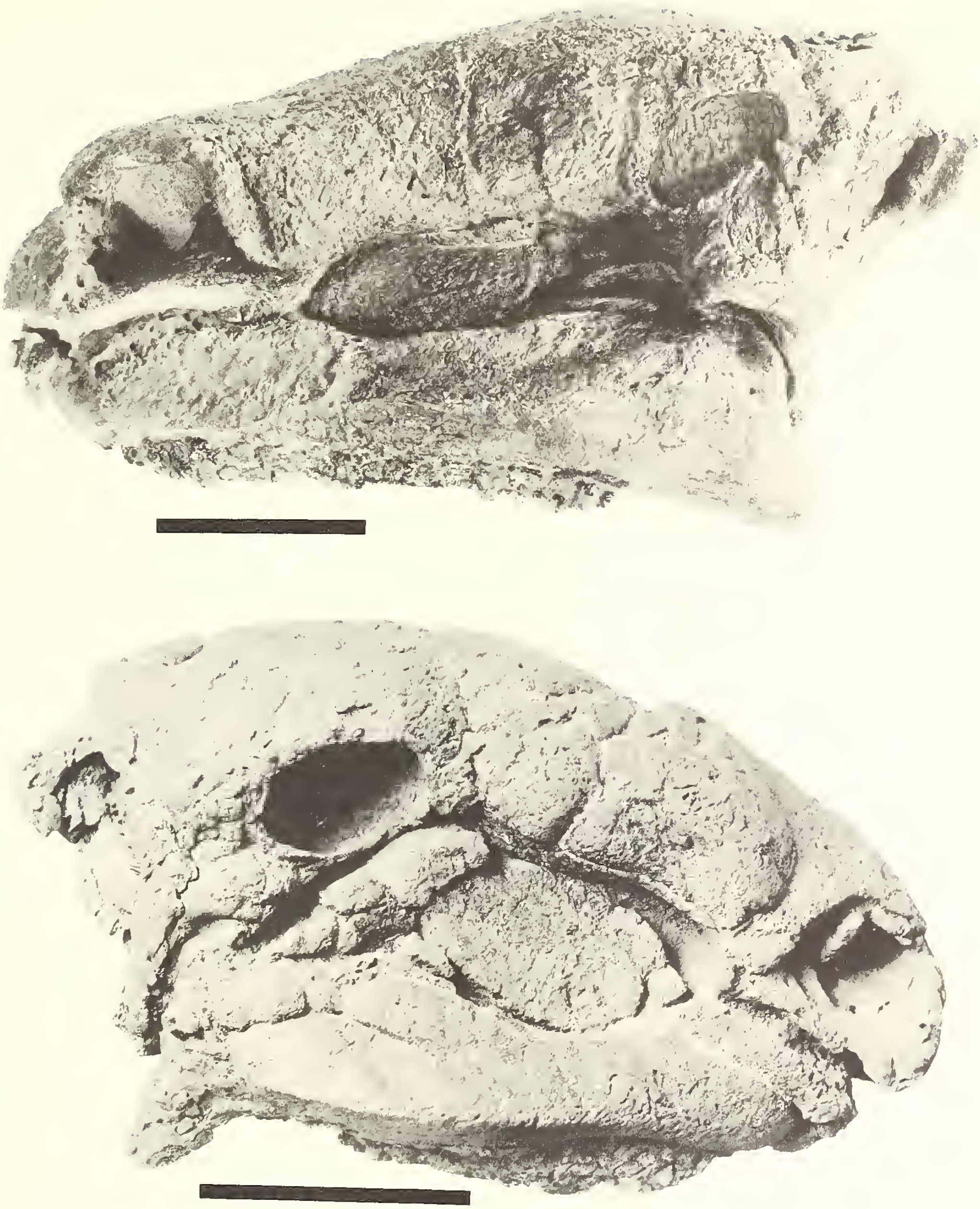
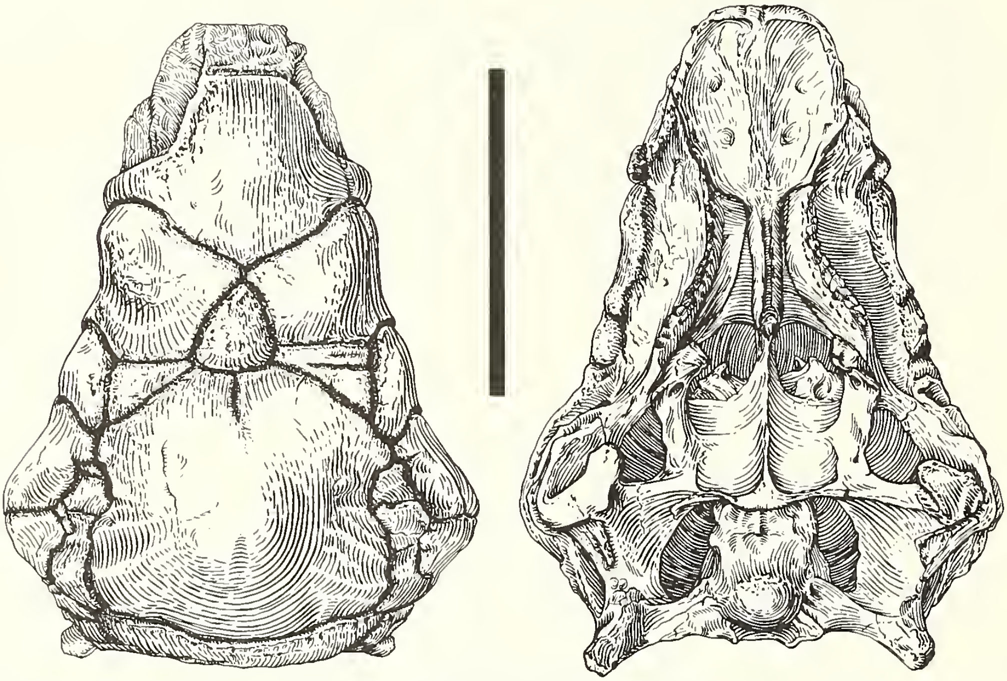
EXPLANATION OF PLATE 12

Upper: AMNH 5381, *Panoplosaurus*, skull and mandible; lateral view. *Lower*: NMC 2759, *Panoplosaurus mirus* (type specimen), skull and mandible; lateral view. Length of reference line = 10 cm.



COOMBS, ankylosaur dinosaurs

pterygoid-basiphenoid contact is not fused (exception: new Asiatic genus; Maryańska MS.). A backwardly opening foramen magnum and an oval, usually flat occipital condyle suggest that in life the head and neck had their long axes aligned as seen in lateral view. In most Ankylosauridae the quadrate, squamosal, and paroccipital process have articulation-like contacts (exception: bones are fused in a new Asiatic genus; Maryańska MS.).



TEXT-FIG. 4. ROM 1215, *Panoplosaurus*, skull; dorsal and ventral views. Length of reference line = 20 cm.

Nodosauridae: nodosaurid palates are narrow and terminate anteriorly with a round to oval, commonly elongate premaxillary plate (text-fig. 4). A ridge connects the cutting edge of the premaxillae to the anterior end of the maxillary tooth row. Some genera have no secondary palate posterior to the premaxillae (e.g. *Sauropelta*, text-fig. 6C). Other genera have a single horizontal plate between the teeth (e.g. *Panoplosaurus*, text-figs. 4 and 6A, B). Nodosaurid pterygoids have a wide central plate with massive mandibular rami that arise laterally and project anteriorly approximately parallel to the midline (text-fig. 4B). In all known nodosaurid skulls the pterygoid and basisphenoid are fused together. A roughly spherical occipital condyle is set on a short, ventrally directed neck, and the foramen magnum opens somewhat ventrally suggesting that in life the skull was carried at a downward angle to the neck. Quadrate, squamosal, and paroccipital process are fused together in all Nodosauridae.

Skull: respiratory tract and cranial sinuses

Ankylosauria in general: the respiratory tract has no distinguishing features at the subordinal level.

Ankylosauridae: all ankylosaurids have complexly folded respiratory pathways within the cranium (text-fig. 5). Also, there is an extensive system of pouches and sinuses that are bounded both by normal cranial elements (vomers, maxillae, premaxillae, etc.) and by new ossifications unknown in other fossil Reptilia (Maryańska MS.).

Nodosauridae: nodosaurids have simple paired respiratory passages within the cranium with no development of pouches or sinuses (text-fig. 6).

Teeth

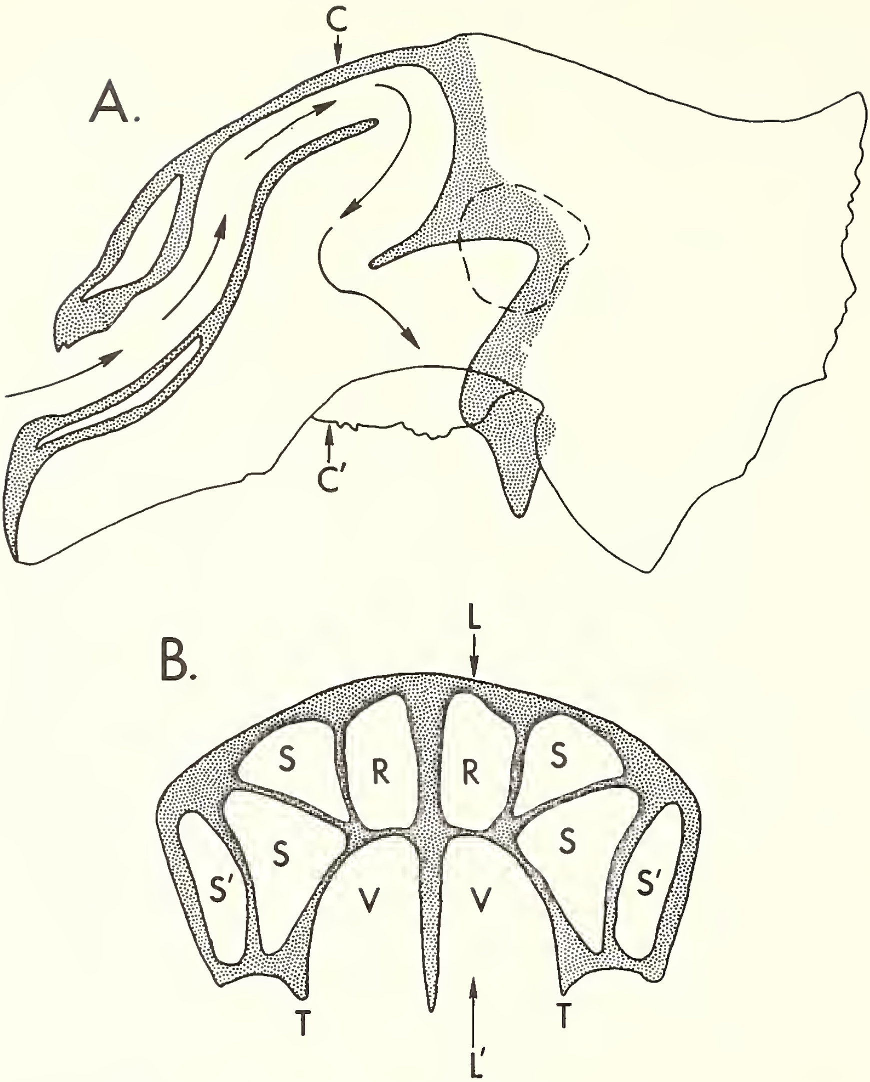
Ankylosauria in general: ankylosaur teeth are very small relative to skull size, with tiny crowns set on long, straight roots. Crowns are leaf-shaped, laterally compressed, and have equal numbers of cusps along anterior and posterior edges. Flanks of the crown are grooved or fluted and enamel is equally thick on labial and lingual surfaces. There are relatively few functional teeth in each maxilla and there are no more than two or three rows of replacement teeth. Adjacent teeth do not interlock to form a solid battery and do not align to form a single cutting edge. Ankylosaurs, along with stegosaurs and pachycephalosaurs, have the simplest and presumably most primitive teeth and tooth battery system among the Ornithischia.

Ankylosauridae: crowns of ankylosaurid teeth are very small both relative to their long roots and relative to skull size. Bases of the teeth are commonly swollen, but a distinct cingulum is rare. Fluting of the sides may be complex (e.g. *Euoplocephalus*). Premaxillary teeth are unknown in the Ankylosauridae.

Nodosauridae: nodosaurid teeth have larger crowns relative to root and skull size than ankylosaurid teeth. Bases of the crowns are only slightly inflated and well-defined basal cingula are common. Lateral fluting usually takes the form of parallel grooves that arise between cusps along the upper edge of the crown. *Sauropelta* (AMNH 3035), *Silvisaurus* (Eaton 1960), and possibly *Struthiosaurus* (Nopcsa 1928) have premaxillary teeth, but *Panoplosaurus* (Lambe 1919; Sternberg 1928; Gilmore 1930; Russell 1940) does not.

Vertebral column

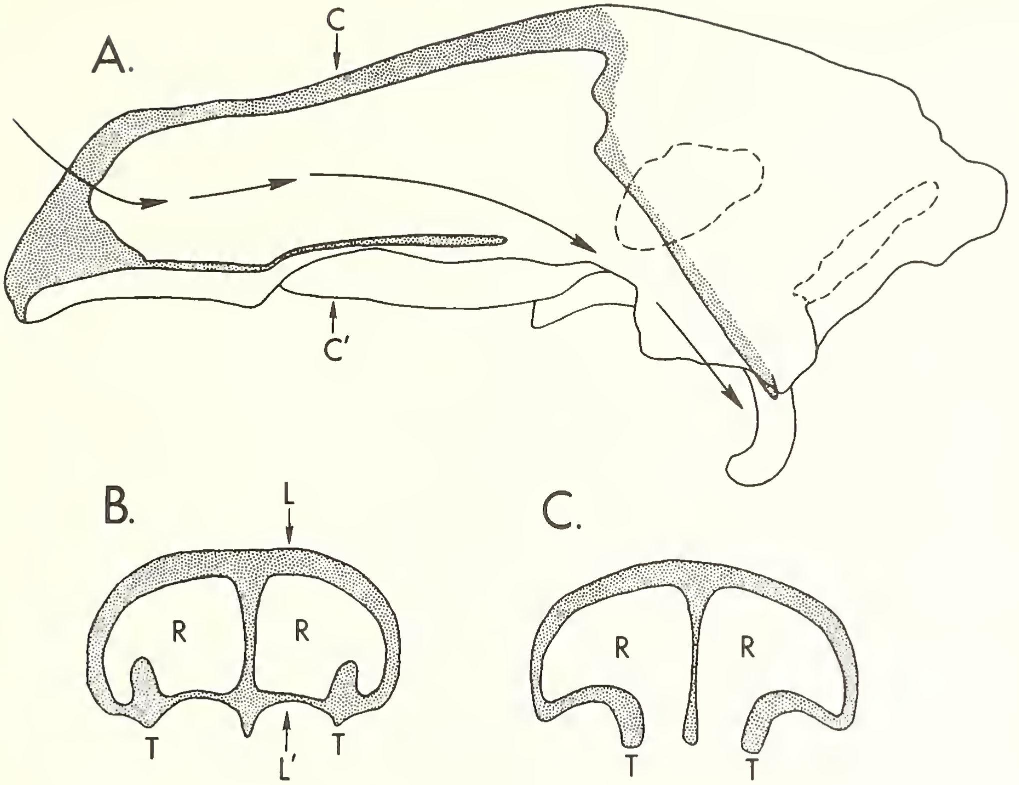
Ankylosauria in general: ankylosaur vertebral centra have expanded, amphiplatyan to amphicoelous articular faces. Neural arches are low and neural spines are moderately tall. Centra of presacral vertebrae have lengths subequal to their maximum diameters; most caudal centra are shorter than their diameters. Transverse processes of dorsal vertebrae are inclined upwards and outwards, but not to the degree seen in *Stegosaurus*, and dorsal ribs, T-shaped in section, are commonly fused to both transverse process and centrum. The last four or five dorsals co-ossify and fuse to the sacrum to form a presacral rod. Ribs fused to the presacral rod contact and help support the hypertrophied pre-acetabular process of the ilium. One or two proximal caudals are sometimes fused to the sacrum and commonly have massive transverse processes that contact the abbreviated postacetabular process of the ilium (text-fig. 12).



TEXT-FIG. 5. Diagrammatic sections through *Euoplocephalus* skulls showing respiratory passages and cranial sinuses. Based on several specimens.

A, parasagittal section with main respiratory path indicated by arrows and position of orbit indicated by broken line. B, cross-section. Abbreviations: C–C′, level of cross-section shown in B; L–L′, level of parasagittal section shown in A; R, main respiratory tract; S, cranial sinus; S′, maxillary sinus; T, tooth row; V, palatal vault.

Ankylosauridae: articular faces of most ankylosaurid centra are flat, but a few posterior dorsals may have a centrally positioned knob on the articular face. Atlas and axis are separate in *Pinacosaurus* and *Euoplocephalus* but are fused in other genera (new Asiatic genus; Maryańska MS.). Distal caudal vertebrae are large and highly modified in connection with presence of a tail club. Long prezygapophyses

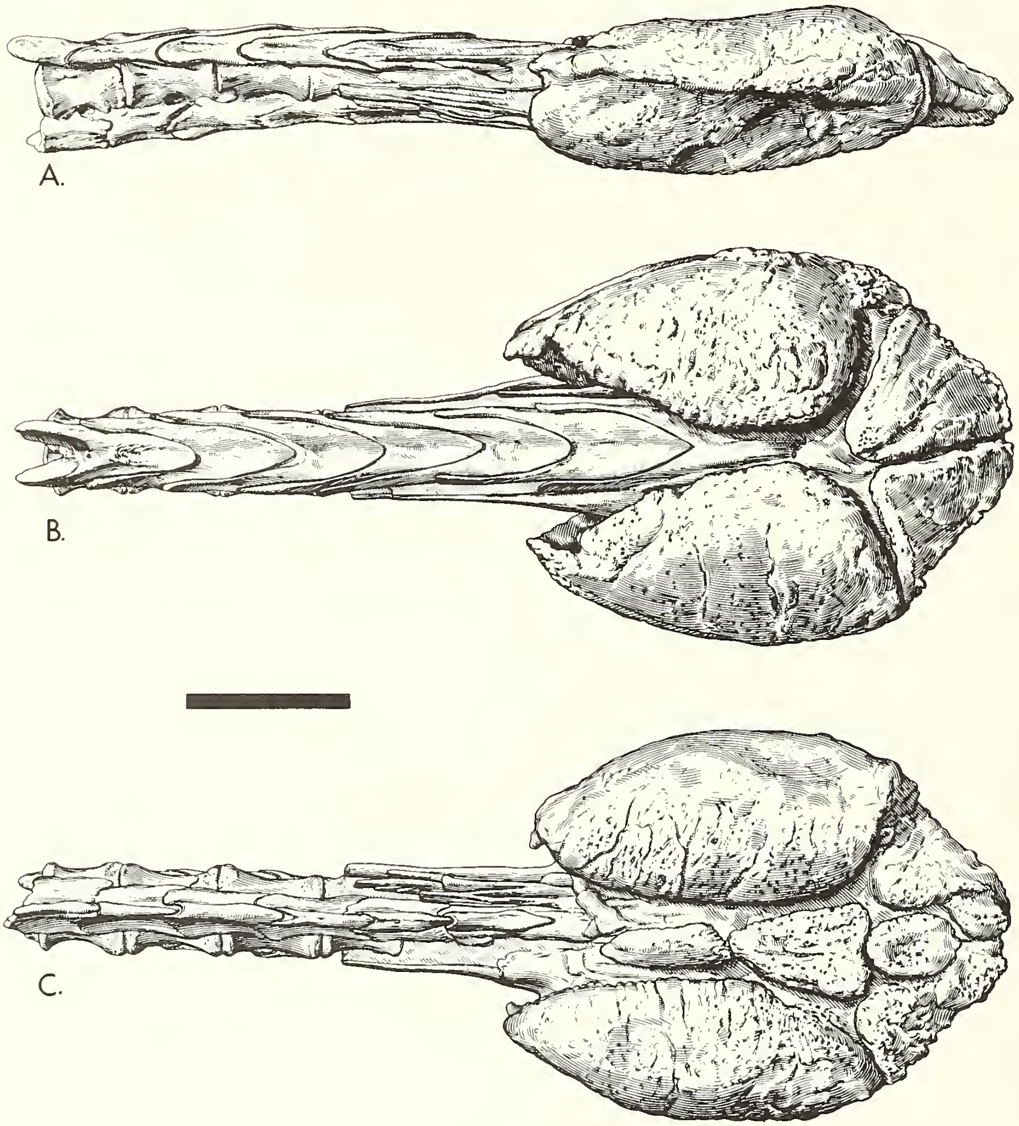


TEXT-FIG. 6. Diagrammatic section through nodosaurid skulls showing respiratory passages. A, parasagittal section based on several *Panoplosaurus* skulls. The respiratory path is shown by arrows. Positions of the eye and lateral temporal fenestra indicated by broken lines. The nostril lies lateral to the plane of this section and thus the respiratory tract appears to be closed anteriorly. B, cross-section through the snout of *Panoplosaurus*, based primarily on AMNH 3076. Ridges protruding into the respiratory passages contain enamel organs, replacement teeth, and roots of functional teeth. C, cross-section through the snout of *Sauropelta*, restored from the badly crushed skull of AMNH 3035. *Sauropelta* lacks a secondary palate posterior to the premaxillary shelf. Abbreviations: C–C′, level of cross-sections shown in B and C; L–L′, level of parasagittal section shown in A; R, respiratory tract; T, tooth row.

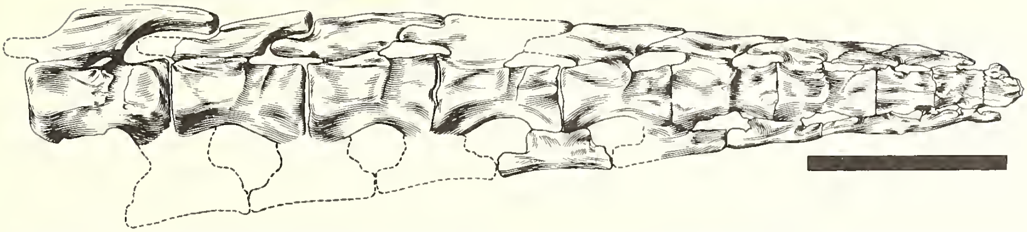
and long flattened postzygapophyses of posterior caudals extensively overlap one another and effectively immobilize the distal third of the tail (text-fig. 7). Neural arches of distal caudals, measured from the extreme tips of pre- and postzygapophyses, may be twice the length of their centra. Haemal arches of distal caudals are low, elongate, tube-like, and have zygapophyseal-like interlocking articulations (text-fig. 7A, C). In some specimens the centra of posterior dorsals fuse into a solid rod (Maryańska 1969).

Nodosauridae: posterior dorsal and proximal caudal vertebrae of nodosaurids usually have a median, knob-like projection on the articular faces of the centra (notochordal projection of Gilmore 1930). Atlas and axis vertebrae may be fused

(*Panoplosaurus*) or free (*Sauropelta*, *Struthiosaurus*). Caudal vertebrae are progressively smaller towards the distal, clubless end of the tail (text-fig. 8). Zygapophyses of distal caudals are relatively much shorter than in Ankylosauridae. There is contact between successive haemal arches through about the distal half of a nodosaurid tail, but there are no interdigitating articulations, and the arches extend further from their centra than in Ankylosauridae (text-fig. 8).



TEXT-FIG. 7. AMNH 5214, *Ankylosaurus magniventris*, distal caudal vertebrae with terminal tail club. A, lateral view. B, dorsal view. C, ventral view. Length of reference line = 20 cm.

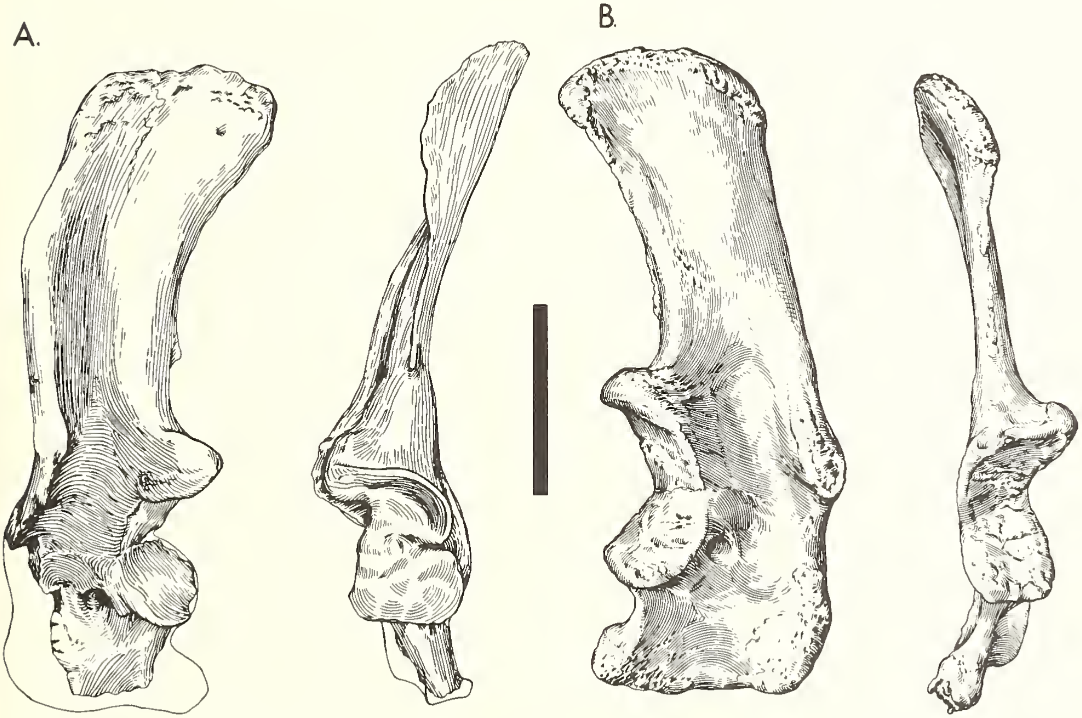


TEXT-FIG. 8. AMNH 3032, *Sauropelta edwardsi* (type specimen), distal end of tail. Length of reference line = 10 cm.

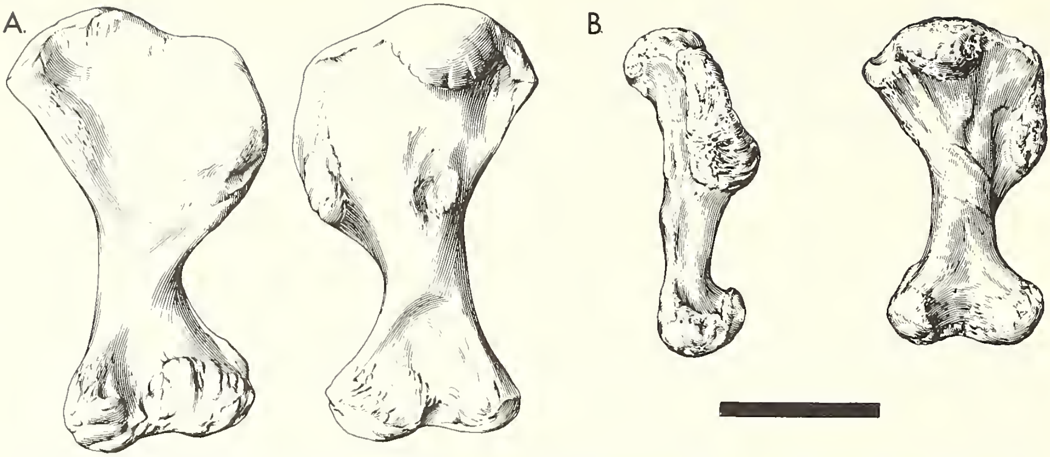
Pectoral girdle and forelimb

Ankylosauria in general: in most ankylosaurs the scapula and coracoid are co-ossified (exceptions: *Struthiosaurus*, *Hylaeosaurus*). The massive forelimbs are two-thirds to three-quarters the length of the hindlimbs. A long olecranon process accounts for one-quarter to one-third the entire length of the ulna.

Ankylosauridae: ankylosaurid scapulae are relatively long, the coracoids relatively small compared with nodosaurid elements. There is a ridge-like spine along the extreme anterior edge of the scapula (text-fig. 9). A pair of roughly triangular sternal



TEXT-FIG. 9. A, AMNH 5895, *Ankylosaurus magniventris* (type specimen), scapulocoracoid; lateral and posterior views. B, AMNH 5424, *Euoplocephalus*, scapulocoracoid; lateral and posterior views. Length of reference line = 20 cm.



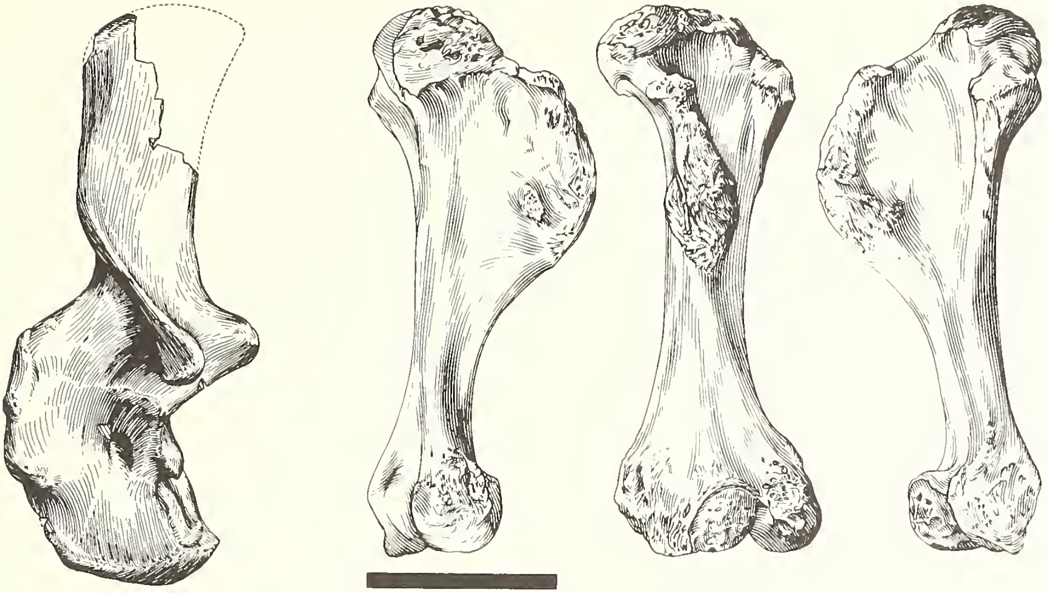
TEXT-FIG. 10. A, AMNH 5214, *Ankylosaurus magniventris*, left humerus; ventral and dorsal views. B, AMNH 5404, *Euoplocephalus*, right humerus; lateral and dorsal views. Length of reference line = 20 cm.

plates is fused along the ventral midline to form a single, rhomboidal plate (Maleev 1954, fig. 6). Massive ankylosaurid humeri have a very large pectineal crest that usually terminates at or slightly distal to humeral mid-length (text-fig. 10). A rather flat radial capitulum on the humerus has an oval outline that corresponds to the oval cross-section of the radius.

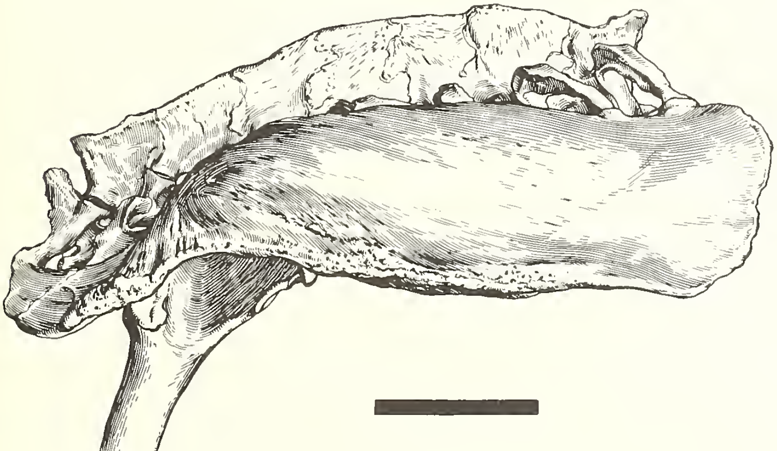
Nodosauridae: nodosaurid scapulae are relatively short and slender and the coracoids relatively very large compared with ankylosaurid elements (text-fig. 11). A knob-like scapular spine overhangs the coracoid and is positioned either centrally on the scapular blade or far posteriorly near the glenoid notch (text-fig. 11). Anterior to the scapular spine is a supraspinous fossa formed by coracoid and scapula. In the primitive nodosaurid *Hylaeosaurus* the scapular spine is positioned posteriorly, near the glenoid, but is ridge-shaped rather than knob-like and there is no supraspinous fossa. Nodosaurid sternal plates are narrower than ankylosaurid plates and are not fused along the midline (Eaton 1960, incorrectly identified as a pubis, see Ostrom 1970, p. 114). Nodosaurid humeri appear longer and more slender than those of ankylosaurids primarily because the pectineal crest commonly terminates more proximally (text-fig. 11). The radial capitulum is a subspherical knob that rises well above the humeral shaft, and the radius is almost circular in cross-section.

Pelvic girdle and hindlimb

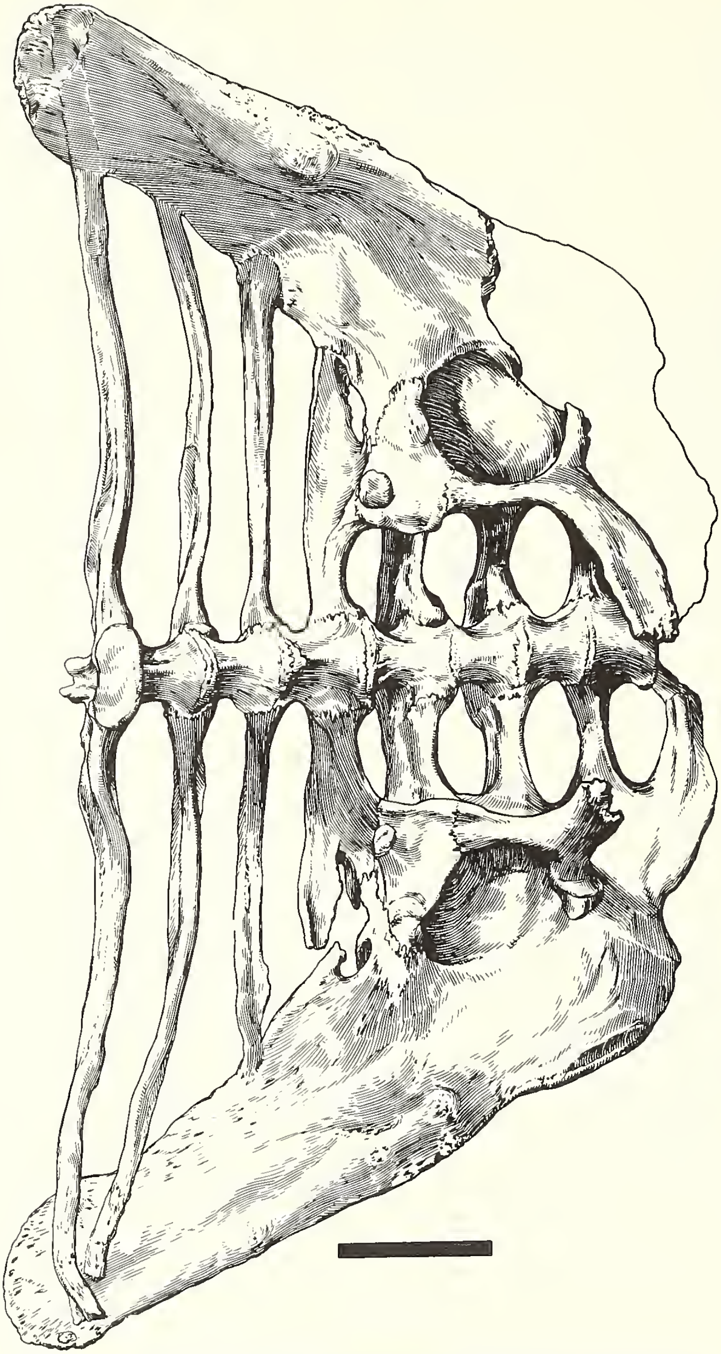
Ankylosauria in general: ankylosaur ilia are twisted so that the primitive lateral surface faces ventrally or ventromedially and the ilium overhangs the femur (text-figs. 12–14). The pre-acetabular segment of the ilium is very long and diverges from the vertebral column anteriorly (text-fig. 12); the postacetabular segment is short. The tiny, block-like pubis has a short, finger-like postpubic process but no distinct prepubic process. The acetabulum, which is always imperforate, is formed almost entirely by ilium and ischium (illustrations of ankylosaur pelves given by Brown 1908 and von Huene 1956, are incorrect). The massive femur is 30% longer than the equally massive tibia.



TEXT-FIG. 11. *Left*: YPM 5179, *Sauropelta edwardsi*, scapulocoracoid; lateral view. *Right*: AMNH 3032, *Sauropelta edwardsi* (type specimen), right humerus; lateral, ventral, and medial views. Length of reference line = 20 cm.



TEXT-FIG. 12. AMNH 5409, *Euoplocephalus*, pelvic girdle; lateral view of right side. Length of reference line = 20 cm.



TEXT-FIG. 13. AMNH 5409, *Euoplocephalus*, pelvic girdle; ventral view. Length of reference line = 20 cm.

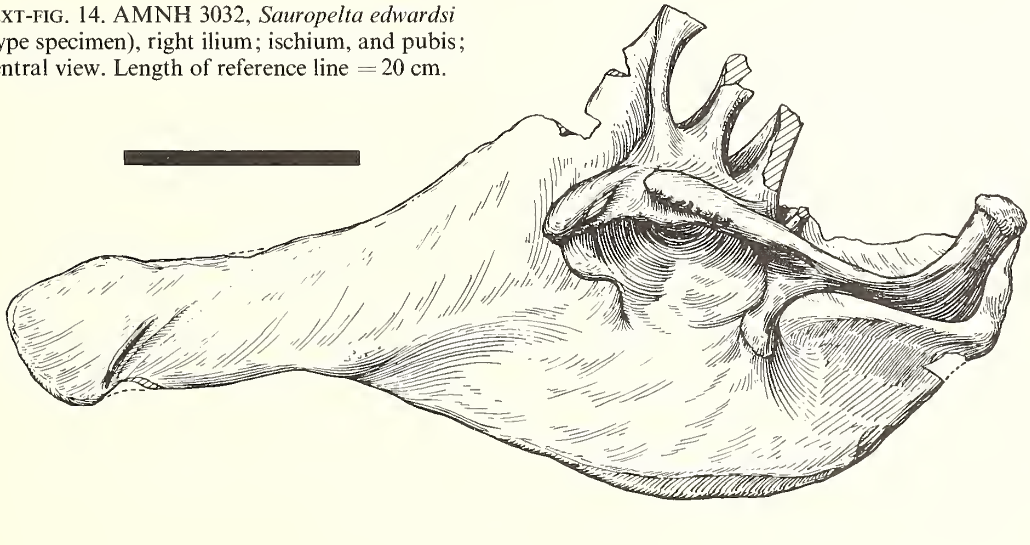
Ankylosauridae: the pre-acetabular segment of the ilium of ankylosaurids is broad and twisted such that the primitive lateral surface faces ventromedially. The post-acetabular segment of the ilium is very short (text-fig. 12). A straight or slightly curved ischium descends almost vertically from the acetabulum (text-fig. 13). There is little distinction between the terminally positioned femoral head and the proximal femoral trochanters (text-fig. 15). Insertion of the coccygeofemoralis muscles (fourth trochanter) is distal to the femoral mid-length (text-fig. 15).

Nodosauridae: in nodosaurids the pre-acetabular segment of the ilium is somewhat shorter and narrower and the postacetabular segment somewhat longer than in ankylosaurids (text-fig. 14). The pre-acetabular part is twisted into a horizontal plane and consequently the primitive lateral surface faces ventrally. Nodosaurid ischia extend postero-ventrally from the acetabulum and have a sharp flexion near the middle that turns the distal end straight downwards (text-fig. 14). There is a slight displacement of the femoral head medially, and proximal femoral trochanters are more distinct than in ankylosaurids (text-fig. 16). The fourth trochanter is always on the proximal half of the femur.

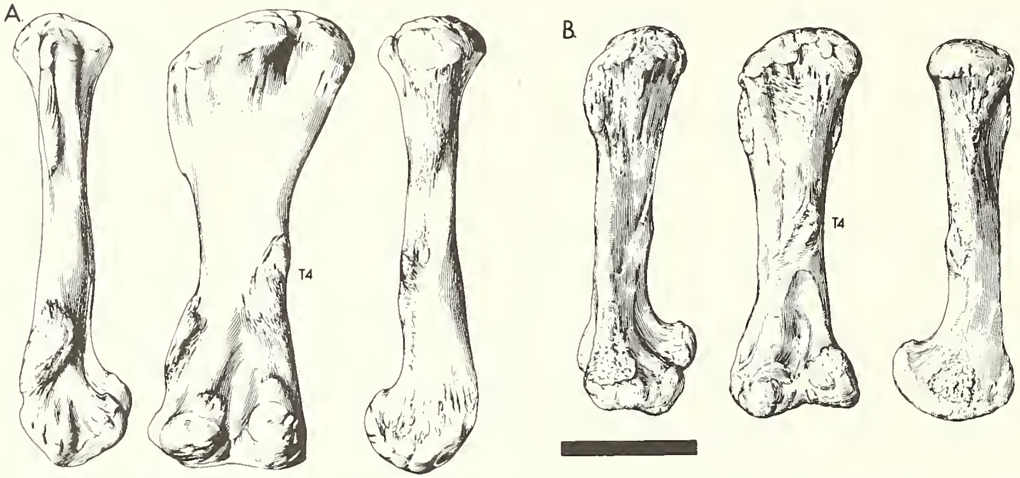
Postcranial armour

Ankylosauria in general: ankylosaurs have an extensive postcranial armour composed of oval keeled plates set into a continuous, mosaic of interlocking small, flat ossicles. Keeled plates are commonly arranged in transverse rows and keels of larger plates may be higher and sharper towards the flanks of the body. Anteriorly, the first two transverse rows of plates are fused to underlying half-rings of bone to form two cervical half-rings. Median dorsal plates of the third transverse row are fused together in some genera (e.g. *Panoplosaurus*). Brown (1908) restored *Ankylosaurus* with longitudinally arranged keeled plates, and Nopcsa (1929) restored *Struthiosaurus* with seven anterior cervical collars and numerous caudal rings, but both of these restorations are entirely hypothetical and unsubstantiated.

TEXT-FIG. 14. AMNH 3032, *Sauropelta edwardsi* (type specimen), right ilium; ischium, and pubis; ventral view. Length of reference line = 20 cm.

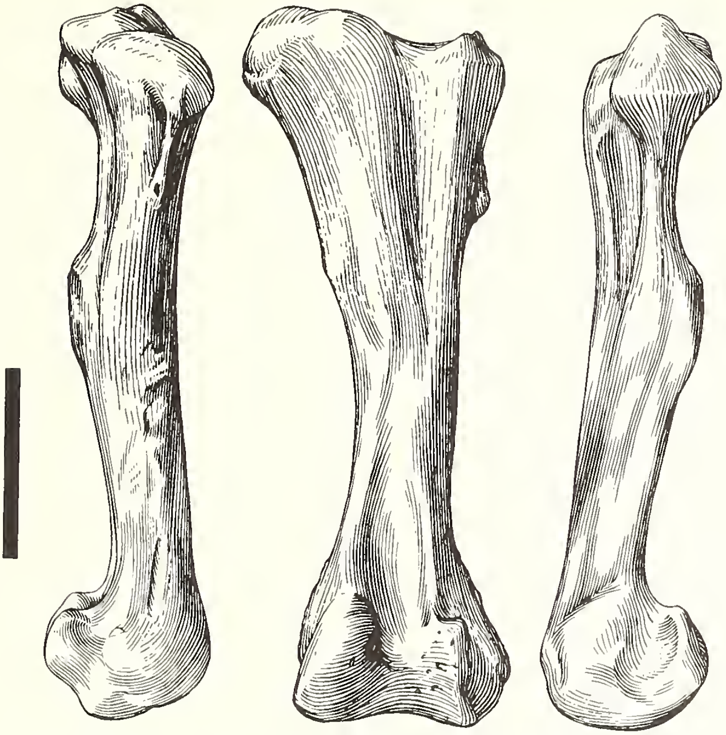


Ankylosauridae: oval keeled plates of ankylosaurids are deeply excavated on the inner surface so that the plates are relatively thin and light. Median keels of these plates may be tall, but plate height never exceeds maximum basal diameter. Some plates are shaped like low, obtusely pointed cones that have been laterally compressed. Cross-sections of such plates are lenticular or lozenge-shaped. Keeled dermal plates fused to cervical half-rings do not contact each other and retain the typical oval outline of keeled plates from other areas of the body. Two massive plates which may be blunt or pointed, and a variable number of smaller ossicles form a large, terminal tail club (text-fig. 7).



TEXT-FIG. 15. A, AMNH 5214, *Ankylosaurus magniventris*, left femur; lateral, posterior, and medial views. B, AMNH 5404, *Euoplocephalus*, left femur; lateral, posterior, and medial views. Position of fourth trochanter is indicated at T4. Length of reference line = 20 cm.

Nodosauridae: inner surfaces of nodosaurid keeled plates are flat or only slightly excavated and the plates are therefore thicker and heavier than similar ankylosaurid plates. In addition to oval keeled plates and compressed conical plates, nodosaurids have tall conical spikes or spines that have heights at least twice the maximum basal diameter and that are oval to circular in cross-section. Some of these spines formed a low horizontal row along the side of the body (Matthew 1922). Some Nodosauridae also have taller spikes with heights of up to five times their basal diameter and which are very similar to *Stegosaurus* caudal spines. Where these spikes were positioned on nodosaurids is uncertain, but limited evidence suggests they were on the flanks of the body and not on the tail. Keeled plates of nodosaurid cervical half-rings contact each other and are rectangular or square in outline. Nodosaurids do not have a tail club.



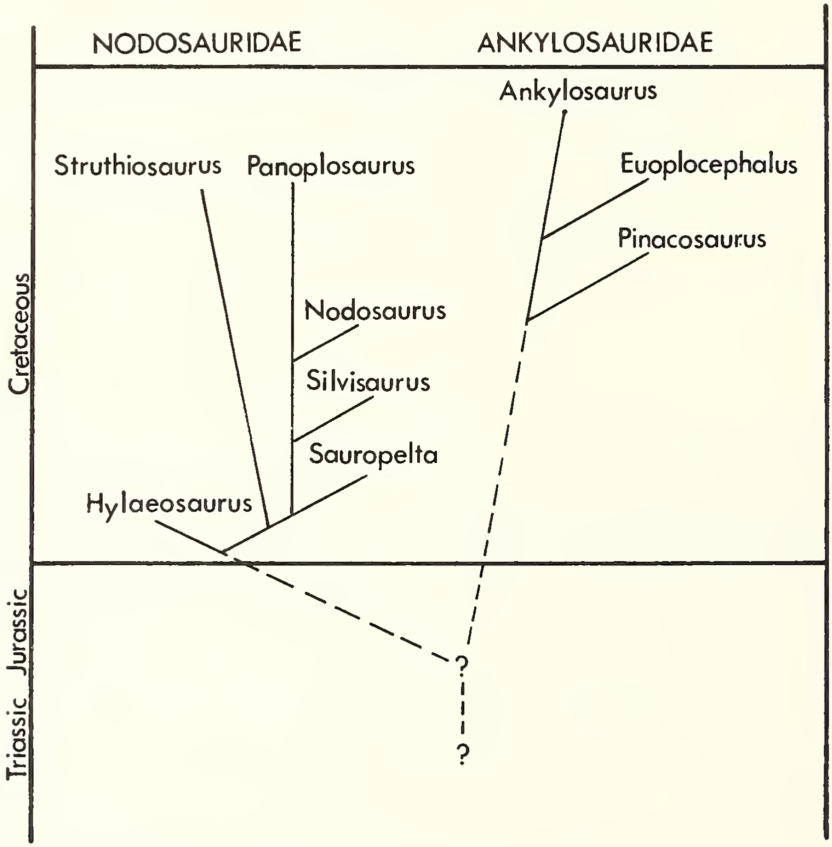
TEXT-FIG. 16. AMNH 3032, *Sauropelta edwardsi* (type specimen), left femur shown reversed; lateral, posterior, and medial views. Length of reference line = 20 cm.

DISTRIBUTION AND EVOLUTION

Ankylosaurians are present in most Cretaceous formations that yield dinosaurs (see Appendix B for complete list with references), but are unknown in Jurassic formations. The distribution of the two families is different. Nodosauridae are present in Europe from Neocomian (Wealden Beds) to Campanian (Middle Gosau Beds and Ajka Beds) and are present in North America from Neocomian or Aptian (Arundel Formation to Campanian or earliest Maestrichtian (Mbr. A of Edmonton Formation and Bearpaw Shale). There is a single tooth (AMNH 5008) from the late Maestrichtian (Hell Creek Formation) that may belong to a nodosaurid. Nodosauridae are not present in Asia. Ankylosauridae are present in Asia from Coniacian or Santonian (Djadochta Formation) to late Campanian or early Maestrichtian (Upper Nemget Formation) and are present in North America from Campanian (Two Medicine Formation, Judith River Formation, Oldman Formation) to late Maestrichtian (Hell Creek Formation, Mbr. E of Edmonton Formation). Ankylosauridae are not present in Europe. Ankylosaur specimens from South America ('Estratos con Dinosaurios') are too fragmentary for positive assignment to one of the two families.

Evolution of the Nodosauridae is very conservative, with little morphologic diversity. The six genera that are known from reasonably complete material can be arranged into three groups or lineages (text-fig. 17). *Hylaeosaurus* is unique and primitive among Nodosauridae in lacking a supraspinous fossa. The scapular spine is displaced posteriorly as in all Nodosauridae, but muscular changes leading to formation of the supraspinous fossa have not developed. *Hylaeosaurus* is also primitive in having the scapula and coracoid separate rather than fused together, a feature shared with *Struthiosaurus*. The small size of the type specimen of *Hylaeosaurus* is responsible for the erroneous idea that the genus is small (e.g. Romer 1956, 1968; Steel 1969). Isolated elements referable to *Hylaeosaurus* (e.g. BM (NH) R1106, R1107, 2602a, and 2615) indicate a maximum size approaching that of the largest Nodosauridae.

Struthiosaurus appears to be the terminus of a European lineage that is represented in the early Cretaceous by specimens described under the name '*Acanthopholis*' (here regarded as a *nomen dubium*). These nodosaurids are characterized by small size, premaxillary teeth (?), and a separate coracoid and scapula. Unlike *Hylaeosaurus*



TEXT-FIG. 17. Relationships of the major genera of the Ankylosauria.

there is a fully developed supraspinous fossa. Whether the small size (about one-quarter in linear dimensions the size of typical North American Nodosauridae) of this *Struthiosaurus* group is primitive (Romer 1956, 1968; Steel 1969) or secondary is unclear. There does not appear to be an over-all trend towards large size in the Nodosauridae in so far as the earliest North American genus (*Sauropelta*, Aptian or Albian, Cloverly Formation) is one of the largest nodosaurids. The concept that *Struthiosaurus* and '*Acanthopholis*' are more lightly armoured (Romer 1956, 1968; Steel 1969) than North American nodosaurids is incorrect. The extent to which armour covers the body is about the same in all Nodosauridae.

North American Nodosauridae form a third group characterized by uniformly large size, co-ossified coracoid and scapula, and fully developed supraspinous fossa. Early forms (*Sauropelta* and *Silvisaurus*; text-fig. 17) retain premaxillary teeth, but these are lost in late Cretaceous *Panoplosaurus*. *Panoplosaurus* is also advanced in that the atlas and axis vertebrae are fused, whereas these vertebrae are separate in most ankylosaurs (*Sauropelta*, *Struthiosaurus*, and the ankylosaurids *Pinacosaurus* and *Euoplocephalus*).

Unique derived characters that distinguish nodosaurids from all other Ornithischia, including Ankylosauridae, include fusion of the squamosal, paroccipital process, and dorsal end of the quadrate; a scapular spine displaced posteriorly to near the glenoid notch; and a sharp flexion near mid-length of the ischium. Because of these features, no member of the Nodosauridae is morphologically suitable as an ancestor for the Ankylosauridae.

Three genera of the Ankylosauridae are known from reasonably complete specimens, and these indicate an even more conservative evolution than in the Nodosauridae. When arranged according to relative geologic age (text-fig. 17), there is a regular size increase from *Pinacosaurus* through *Euoplocephalus* to *Ankylosaurus* (maximum skull lengths, respectively = 305, 460, and 760 mm). *Ankylosaurus* was the last and largest of all the Ankylosauria. *Pinacosaurus* retains in its pes the primitive ornithischian phalangeal formula of 2-3-4-5-(?)0, while *Euoplocephalus* is advanced in having lost pes digit 1 including the metatarsal. In *Pinacosaurus* and *Euoplocephalus* the nostril is an elongate slit divided by a vertical septum that separates the main respiratory path from a more lateral maxillary sinus, and the premaxillae of these genera are not covered by dermal plates (see lateral view in text-fig. 3). In *Ankylosaurus* the nasal bone and/or a dermal plate fused to the dorsal margin of the nostril has expanded anteriorly and laterally over the narial opening and premaxillae. Thus in *Ankylosaurus* the premaxillae are covered by dermal plates and the nostril is a small circular opening that lies far laterally on the snout (Pl. 12).

Unique derived characters that distinguish ankylosaurids from all other Ornithischia, including Nodosauridae are: horn-like projections formed by dermal plates at the postero-lateral corners of the skull roof; lateral temporal fenestrae hidden below expanded quadratojugal and co-ossified dermal plates; a complex system of cranial sinuses; and a terminal tail club supported by highly modified distal caudal vertebrae. Because of these features, no member of the Ankylosauridae is morphologically suitable as an ancestor for the Nodosauridae.

Because all genera of the Ankylosauridae and all genera of the Nodosauridae have derived characters diagnostic of their respective families, it might reasonably be questioned whether the two families of the Ankylosauria have a common ancestry. However, the families Ankylosauridae and Nodosauridae share the following unique derived characters that set them apart from other Ornithischia and justify their unification in a suborder Ankylosauria: skull covered by co-ossified dermal plates; upper temporal fenestrae closed by encroachment of surrounding skull bones and co-ossified dermal plates; postorbital shelf formed; presacral rod formed; ilia twisted into horizontal plane; pre-acetabular ilium long and broad; block-like pubis with short, finger-like postpubic process and no distinct prepubic process; and extensive armour of keeled plates includes two cervical half-rings with co-ossified keeled plates. The only one of the preceding features that is found in other ornithischians is closure of the upper temporal fenestrae, which has taken place independently in pachycephalosaurs (Brown and Schlaikjer 1943; Galton 1971; Maryańska and Osmolska 1974). Therefore the Ankylosauridae and Nodosauridae must have some unknown common ancestor, probably in the pre-Cretaceous Mesozoic (text-fig. 17). Phylogenetic divergence of the two families, and evolution of the numerous morphologic differences between them are not documented by currently known fossils.

If the common ancestor of the two ankylosaur families is unknown, the origin of the Ankylosauria as a whole is even more obscure. *Scelidosaurus* has been proposed as an ancestral ankylosaur on the basis of its exceedingly short prepubic process (Romer 1968; Thulborn 1971*a*), an opinion based upon a referred specimen (Rixon 1968; Charig 1972) that may not belong to *Scelidosaurus*. The pelvis of this alleged *Scelidosaurus* has a long postpubic process, a perforate acetabulum, a short, pointed pre-acetabular ilium, and a broad, vertical postacetabular ilium (Charig 1972, fig. 2), all features unlike ankylosaur pelvic structure. Overall, the pelvis of this alleged *Scelidosaurus* is more reminiscent of hypsilophodontid Ornithopoda (Thulborn 1974), except that the short prepubic process is similar to that of *Protoceratops* (Brown and Schlaikjer 1940). Ankylosaur pubes (Gilmore 1930; Ostrom 1970) bear no special similarity to that of the alleged *Scelidosaurus*. The type of *Scelidosaurus* (*fide* Newman 1968) has ankylosaur-like armour plates, but lacks the diagnostic cervical half-rings. The upper temporal fenestrae of *Scelidosaurus* are open, and there are no armour plates fused to the skull roof (Owen 1863). *Scelidosaurus* has a single supernumerary cranial element above the orbit (Coombs 1972), whereas *Pinacosaurus* and presumably other Ankylosauridae have three (Maryańska 1971). Nodosaurid skull roof composition is unknown. Therefore, *Scelidosaurus* is not morphologically suitable as an ancestor for the family Ankylosauridae, and in so far as no features diagnostic of the Ankylosauria have yet been described in *Scelidosaurus*, I do not accept the genus as an ancestor for any ankylosaurs. (See note added in proof, p. 168.)

Stegosaurs have often been proposed as close relatives of ankylosaurs because both groups are quadrupedal and armoured (Marsh 1889, 1892; Huene 1909; Nopcsa 1915, 1917, 1918, 1923; Hennig 1915, 1924; Lapparent and Lavocat 1955). *Stegosaurus* has three 'palpebrals' (Coombs 1972) or 'supraorbitals' (Gilmore 1914) arranged similarly to those of the ankylosaurid *Pinacosaurus* (Maryańska 1971) but whether this is a derived character shared by stegosaurs and ankylosaurs, an independent development in each suborder, or the retention of a primitive structure is unclear (Coombs 1972). Stegosaur pelvic morphology is strikingly unlike that of ankylosaurs (Romer 1927). Ankylosaurs share with stegosaurs and pachycephalosaurs the simplest and, by inference, most primitive tooth morphology and arrangement within the Ornithischia. Even relatively 'primitive' Ornithopoda such as *Fabrosaurus* (Thulborn 1971*b*), *Heterodontosaurus* (Crompton and Charig 1962), and *Hypsilophodon* (Swinton 1936; Galton 1974) have asymmetrically distributed enamel, precise alignment of teeth, and initial development of close-packing of replacement teeth, the latter eventually developing into the complex tooth-batteries of hadrosaurs. Also, ankylosaurs are the only Ornithischia with an imperforate acetabulum, possibly a retained primitive feature extending back to pseudosuchians.

Therefore, both the ancestry of ankylosaurs and their connection to other Ornithischia, including stegosaurs, is exceedingly remote from all currently known ankylosaur fossils both temporally and morphologically. At present, the origin of ankylosaurs remains an open question.

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Note added in proof. Since this paper went to press an article has been published suggesting the reclassification of *Scelidosaurus* within the Ornithopoda. (Thulborn, R. A. 1977. Relationships of the Lower Jurassic dinosaur *Scelidosaurus harrisonii*. *J. Paleont.* **51,** 725–739, 6 figs.)

APPENDIX A

During the course of this study, I personally examined type specimens of the following ankylosaur taxa:

Acanthopholis horridus Huxley, 1867 (GSM 109046–GSM 109058); *A. eucercus* Seeley, 1869 (SMC 55552–SMC 55557); *A. macrocercus* Seeley, 1869 (SMC B55588–B55609); *A. platypus* Seeley, 1869 (SMC B55449–B55461); *A. stereocercus* Seeley, 1869 (SMC B55558–B55569); *Ankylosaurus magniventris* Brown, 1908 (AMNH 5895); *Anodontosaurus lambei* Sternberg, 1929 (NMC 8530); *Dyoplosaurus acutosquameus* Parks, 1924 (ROM 784); *Dysganus peiganus* Cope, 1876 (AMNH 3974); *Edmontonia longiceps* Sternberg, 1928 (NMC 8531); *Euoplocephalus tutus* (Lambe, 1902) (NMC 0210; originally described as *Stereocephalus tutus*; the generic name *Euoplocephalus* was proposed by Lambe 1910, with *E. tutus* as type species); *Hoplitosaurus marshi* (Lucas, 1901) (NMNH 4752; originally described as *Stegosaurus marshi*; the generic name *Hoplitosaurus* was proposed by Lucas 1902, with *H. marshi* as type species); *Hylaeosaurus armatus* Mantell, 1833 (BM (NH) R3775); *Nodosaurus textilis* Marsh, 1889 (YPM 1815); *Palaeoscincus asper* Lambe, 1902 (NMC 1349); *P. latus* Marsh, 1892 (YPM 4810); *P. rugosidens* Gilmore, 1930 (NMNH 11868; same as *Edmontonia rugosidens* of Russell, 1940); *Panoplosaurus mirus* Lambe, 1919 (NMC 2759); *Pinacosaurus grangeri* Gilmore, 1933*a* (AMNH 6523); *Polacanthus foxii* Hulke, 1881 (BM (NH) R175; the generic name *Polacanthus* was first used by Huxley 1867, but without a type species or specimen indication); *Priconodon crassus* Marsh 1888 (NMNH 2135); *Priodontognathus phillipsii* Seeley, 1869, 1875 (SMC B53408); *Regnosaurus northamptoni* Mantell, 1848 (BM (NH) R2422; this species may not be an ankylosaur); *Sauropelta edwardsi* Ostrom, 1970 (AMNH 3032); *Scolosaurus cutleri* Nopcsa, 1928 (BM (NH) R5161); *Silvisaurus condrayi* Eaton, 1960 (KU 10296); *Stegopelta landerensis* Williston, 1905 (FMNH UR88); *Struthiosaurus transilvanicus* Nopcsa, 1915 (BM (NH) R4966).

The following casts of type specimens were examined:

AMNH 2062, cast of type of *Heishansaurus pachycephalus* Bohlin, 1953; AMNH uncatalogued cast of type of *Palaeoscincus costatus* Leidy, 1856; AMNH 2071, cast of type of *Peishansaurus philemys* Bohlin, 1953; CM 973, cast of type of *Pleuropeltis suessi* Seeley, 1881; AMNH 2074, cast of type of *Sauroplites scutiger* Bohlin, 1953; AMNH 2070, cast of type of *Stegosaurides excavatus* Bohlin, 1953; CM 972, cast of type of *Struthiosaurus austriacus* Bunzel, 1871.

I have also examined the following specimens:

Referable to (?)*Acanthopholis*: BM (NH) R3774, 35280, 35282, 44581, 49917, 47234, 47234a; GSM JB201, JB202, JB203, JB205, JB206, JB231, JB254, 114581, 114582, 114583, 114584, 114587; SMC B55354–B55358, B55368, B55369, B55370, B55400, B55412, B55436–B55448, B55492, B55514–B55526, B55730, B55731, B55744, B55749, B55750, B55751, B55760–B55765, B55938.

Referable to *Ankylosaurus*: AMNH 5214; NMC 8880.

Referable to *Euoplocephalus*: AMNH 5211, 5216, 5223, 5245, 5266, 5337, 5403, 5404, 5406m, 5409, 5440, 5470; BM (NH) R4947; NMC 349, 2252, 2253, 8876, 31070, 31071, 31072, 31073, 31074; NMNH 7943, 11892, 19747; ROM 788, 813, 832, 833, 1920, 7761, 7763, 7764, 7765, 7766, 7767, 7770.

Referable to *Hylaeosaurus*: BM (NH) R133, R202, R202a, R203, R604a, R643, R695, R1106, R1107, R1875, R1876, R1926, 2047, 2123, 2125, 2188, 2193, 2220, 2417, 2484, 2511, R2538, 2583, 2585, 2587, 2596, 2602a, 2615, 3782, R4951, 28681, 28936, 28949, 34533, 36487, 36489, 36490, 36491, 36492, 36493, 36494, 36515, 36516, 36517, 37713, 37714, 39533.

Referable to *Lametasaurus*(?): AMNH 1959.

Referable to *Panoplosaurus*: AMNH 3072, 3076, 5381, 5665; NMC 317, 8529, 8879, 9492, 9790, 9966; NMC field no. 12–1921; PU 21178; ROM 1215, 3088, 3129, 3302, 3368, 3516, 20892.

Referable to *Sauropelta*: all specimens listed by Ostrom (1970, p. 104) and by Bodily (1969; specimen incorrectly assigned to *Hoplitosaurus*).

APPENDIX B

Listed below are all formations that have yielded ankylosaur remains, with references to important descriptions. An asterisk (*) preceding a formation denotes additional, undescribed ankylosaur material that I have personally examined.

Nodosauridae are present in the following formations (listed alphabetically):

Europe:	Ajka Beds	Nopcsa, 1915, 1929.
	Cambridge Greensand	Seeley, 1869, 1871, 1879; Nopcsa, 1923.
	Chalk Marl	Huxley, 1867.
	Middle Gosau Formation	Bunzel, 1871; Seeley, 1881; Nopcsa, 1918.
	*Wealden Beds	Mantell, 1833, 1841, 1844, 1849, 1850; Owen, 1858; Hulke, 1874, 1881; Nopcsa, 1929.
North America:	*Aguja Formation	All undescribed.
	Arundel Formation	Marsh, 1888; Lull, 1911; Gilmore, 1921.
	*Bearpaw Shale	All undescribed.
	Cedar Mountain Formation	Bodily, 1969.
	Cloverly Formation	Ostrom, 1970.
	Edmonton Formation (Mbr. A)	Sternberg, 1928.
	*Hell Creek Formation	All undescribed, doubtful occurrence.
	*Judith River Formation	Leidy, 1856.
	Lakota Formation	Lucas, 1901, 1902; Gilmore, 1914.
	Mowry Shale or Thermopolis Shale (position uncertain)	Marsh, 1889; Williston, 1905; Moodie, 1910; Lull, 1921.
	Niobrara Formation	Wieland, 1909, 1911; Mehl, 1936.
	Ojo Alamo Formation	Gilmore, 1919.
	*Oldman Formation	Lambe, 1902, 1919; Sternberg, 1921; Russell, 1940.
	Terra Cotta Clay	Eaton, 1960.
	Two Medicine Formation	Gilmore, 1930.
Asia: not present.		

Ankylosauridae are present in the following formations (listed alphabetically):

Europe: not present.		
North America:	*Edmonton Formation (Mbr. A, B, E)	Sternberg, 1929.
	Hell Creek Formation	Brown, 1908.
	*Judith River Formation	All undescribed.
	*Oldman Formation	Lambe, 1902; Gilmore, 1923; Parks, 1924; Nopcsa, 1928.
	*Two Medicine Formation	Gilmore, 1930.
Asia:	Djadochta Formation	Gilmore, 1933*a*; Maleev, 1954; Maryańska, 1971.
	Iren Dabasu Formation	Gilmore, 1933*b*.
	*Lameta Beds	Matley, 1923; von Huene and Matley, 1933; Chakravarti, 1934.
	Upper Nemget Beds	Maleev, 1956; Maryańska, 1969.
	Unnamed strata in the Peoples' Republic of China	Young, 1935; Bohlin, 1953 (many, possibly all specimens described by Young and Bohlin were never catalogued and have deteriorated or disintegrated since they were described: Academia Sinica pers. comm. 1977).

Fragmentary ankylosaur remains that could belong to either family are present in the following formations:

South America:	'Estratos con Dinosaurios'	von Huene, 1929.
North America:	Selma Formation	Langston, 1960.
	Kirtland Formation	Gilmore, 1916, 1935.

A NEW MELIOLOID FUNGUS FROM THE EARLY EOCENE OF TEXAS

by C. P. DAGHLIAN

ABSTRACT. A new species of *Meliolinites* Selkirk, *M. dilcherii*, is reported from the Early Eocene of Texas, U.S.A. The specimens show various stages of perithecial development which are the same as those reported in extant meliolas. This is the oldest known occurrence of the genus.

FUNGI of the family Meliolaceae, usually parasitic on adult leaves, are commonly known as dark mildews. They are found in warm, humid, forested, tropical areas, but may also occur in seasonally dry regions (Yarwood 1973). Fossil melioloid epiphyllous fungi have been reported from the Eocene of Germany (Köch 1939), the Eocene of Tennessee (Dilcher 1965), and the Miocene of Australia (Selkirk 1975). In all cases the fungi were found on angiosperm leaves. Köch (1930) described some material of *Meliola* from the Eocene brown coals of Germany, but little information can be obtained from it because of the incomplete description. Dilcher (1965) was able to distinguish two species of *Meliola*, which have all phases of growth except the perithecial stage. *M. anfracta* Dilcher has the characteristic mycelial setae found in extant meliolas, while *M. spinksii* Dilcher lacks setae, but has other melioloid characters. Selkirk (1975) recognized the fossil genus *Meliolinites* for those forms of epiphyllous fungi which lack setae but otherwise conform to the characters of the Meliolaceae. Selkirk reported one species from New South Wales, *M. nivalis*, with typical spores, mycelia, and hyphopodia. He figured one poorly preserved perithecium of *M. nivalis*, but was unable to observe any taxonomically useful characters. Specimens studied in this report have typical melioloid spores, mycelia, and hyphopodia, as do the species mentioned above. In addition, there are several stages of perithecial development present. This is also the oldest reported occurrence of *Meliolinites* in the fossil record.

Specimens were collected from clay pits of the Elgin-Standard Brick Manufacturing Company, Butler, Texas, located about 50 km east of Austin, Texas in northern Bastrop County. Clay is stripped from the Butler Clay, a basal bed of the Calvert Bluff member of the Lower Eocene Rockdale Formation (Fisher 1961). The Rockdale Formation of the Texas Gulf coast is primarily deltaic sediment and forms over 80% of the Wilcox Group in Texas (Fisher and McGowen 1967). The Calvert Bluff Member contains most of the commercial lignite in central Texas and represents upper delta plain sediments with lignites, deposited in interdistributary regions (Fisher and McGowen 1967; Kaiser 1974). Atlee and others (1968) have suggested interdistributary backswamp or open-lake deposition for the Butler Clay. There are about 5 m of alternating sand, sandy to silty clay, and clay exposed at the pits.

Fungus-bearing leaf fragments were collected from a thin lens of dark grey, fine-grained clay below a layer of ironstone concretions (Irving and Stuessy 1974). Blocks

[Palaeontology, Vol. 21, Part 1, 1978, pp. 171-176, pl. 13.]

of clay were soaked in distilled water to remove the leaf fragments, cleaned in hydrofluoric acid, washed several times, and mounted for light microscopy. Macerations were not needed because the leaves were very light coloured and consisted almost entirely of cuticle with little or no mesophyll tissue.

SYSTEMATIC DESCRIPTION

Family MELIOLACEAE Martin ex Hansford, 1946

Genus MELIOLINITES Selkirk, 1975

Meliolinites dilcherii sp. nov.

Plate 13, figs. 1–6; text-fig. 1

Holotype. The University of Texas Paleobotanical Collection No. 207 (text-fig. 1).

Paratypes. UTPC No. 204 (Pl. 13, fig. 1), UTPC No. 205 (Pl. 13, figs. 2–4), UTPC No. 206 (Pl. 13, figs. 5, 6).

Locality. Butler Clay Member, Rockdale Formation, Wilcox Group. Lower Eocene, Butler, Bastrop County, Texas.

Diagnosis. Species with hyphal branches and capitate hyphopodia alternate to unilateral, rarely opposite; tapered five-celled spores with bipolar germination; lacking mycelial setae and mucronate hypopodia. Mature perithecia at least 155·0 μm in diameter with radiating basal cells, no perithecial appendages.

Beeli formula (modified after Hansford, 1961): 3,(1),–, 1·4,2,2,–.

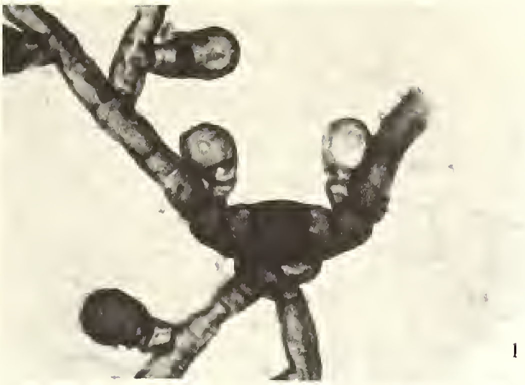
Description. Epiphyllous fungi, colonies 1·5–2·0 mm in diameter, thin to subdense Hyphal branching alternate to unilateral (rarely opposite) at acute angles (45–60°). Hyphal cells 6·6 μm wide, 24·6 μm long, thick walled, straight to slightly sinuous. Capitate hyphopodia 22·0–26·4 μm long, unilateral to alternate, rarely opposite, usually spreading from hyphae at 40–60°, but may be more obtuse. Stalk cells 6·6–11·0 μm long, uniformly 8·8 μm wide, may taper towards the head cells. Head cells 15·4 μm long, 15·4–17·6 μm wide, often with slightly undulate walls. Walls thick, haustorial pore evident in most head cells. No mucronate hyphopodia nor mycelial setae observed. Developing perithecia small globose bodies, 44·0 × 37·5 μm, on base of radiating cells. Mature perithecia 155·0 μm in diameter. No perithecial setae observed. Spores 44·0 × 15·4 μm, four-septate, five-celled, middle cell largest, end cells tapered. Bipolar germination with primary hyphopodia produced from each end cell. Hyphae developed from all cells except the middle one. Occurs on upper epidermis of apparently lauraceous leaves.

Remarks. Spores of *Meliolinites dilcherii* are four-septate, five-celled, and taper towards each end (Pl. 13, fig. 1), a common configuration for the Meliolaceae. Germination is bipolar with each end cell producing a primary hyphopodium.

EXPLANATION OF PLATE 13

Figs. 1–6, *Meliolinites dilcherii* sp. nov. 1, × 500, germinated spore with primary hyphopodia and vegetative mycelium. Note haustorial pores in capitate head cells. 2, × 200, vegetative mycelium showing branching. 3, × 200, 4, × 800, small mass of cells from early stage of perithecial development. 5, × 200, 6, × 800, globose body of cells with radiating hyphae.

PLATE 13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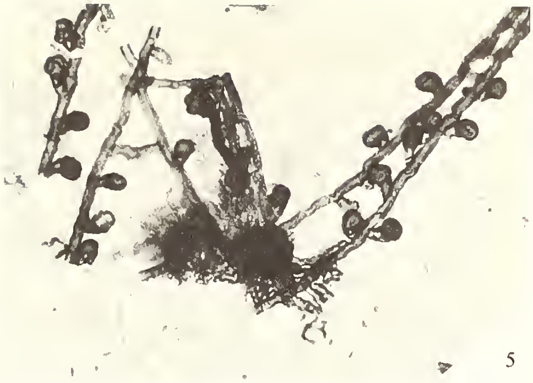
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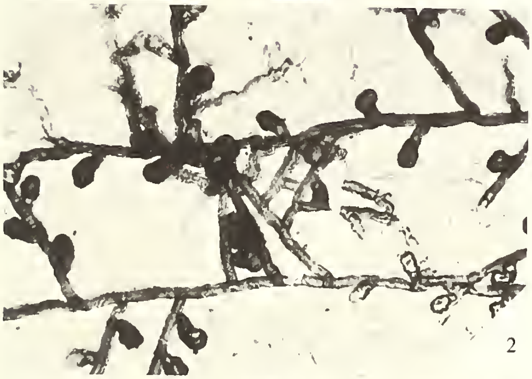
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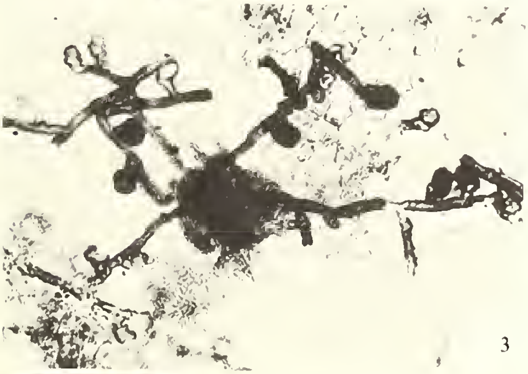
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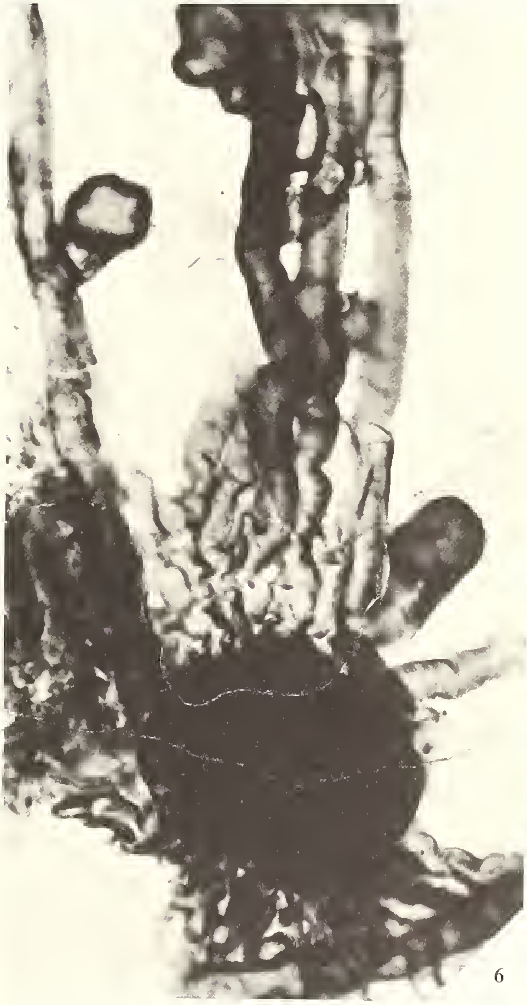
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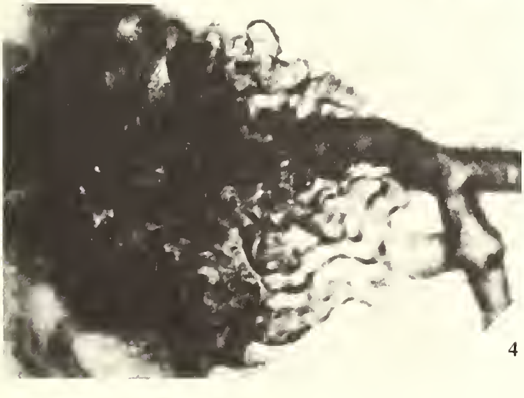
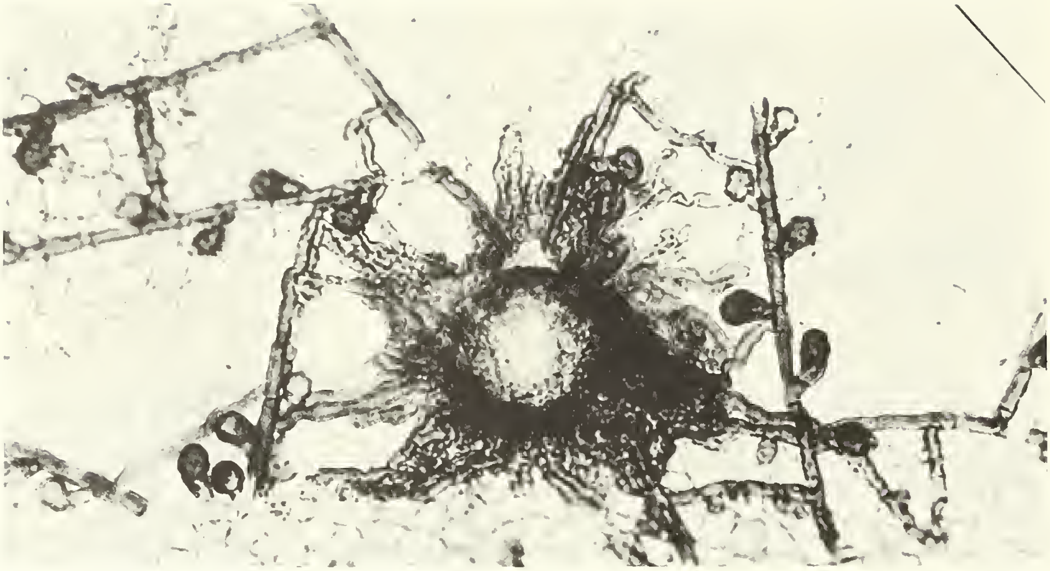

4

DAGHLIAN, Melioloid fungus



TEXT-FIG. 1. Partially crushed mature perithecium with radiating hyphae, ×300.

Primary hyphopodia develop in extant meliolas, with subsequent development arrested unless the spore has landed on an appropriate host (Hansford 1961). This is important, since there seems to be a high degree of host specificity in extant meliolas. Both Dilcher (1965) and Selkirk (1975) found similar specificity in the fossils they studied. Although several extant meliolas have bipolar germination, none of them has spore shapes like *M. dilcherii*. Hyphae are produced from all cells of the spore except the middle one, even from the cells that produced the primary hyphopodia (Pl. 13, fig. 1). Hyphae branch at their distal ends at angles of 45-60°, producing a relatively thin colony, although in some places the hyphae are crowded (Pl. 13, fig. 2). Hyphopodia, each composed of two cells, a short stalk cell and capitate head cell, branch from the hyphae at 40-45°. The hyphopodia are short, modified branches which provide the only connection of the fungus to the host cells. From the centre of each head cell there is a haustorial pore through which the haustorium enters the host cell. No haustoria were found, probably due to their delicate nature.

Several stages in the development of perithecia are present in the material studied. There is, to the author's knowledge, only a single reference to perithecial development in meliolas, that of Graff (1932). A small lateral branch, at first indistinguishable from a capitate hyphopodium, enlarges and divides to produce a small mass of cells. These enlarge and divide further to form the perithecium (Hansford 1961). Cytological details are not clear. The initial mass of cells may produce a radiating layer of cells with or without capitate hyphopodia. The fossil species has several structures which appear to correspond to some of these developmental stages.

The earliest stage represented in the fossil material is one in which the small mass of cells has formed from the perithecial initial. Plate 13, figs. 3, 4 show this as a small cluster of cells near vegetative hyphae. While hyperparasites do occur on meliolas, the similarity between these cells and those of a later stage (Pl. 13, figs. 5, 6) suggests that this is indeed a part of the developing perithecium. The small mass of cells later produces a series of radiating hyphae from beneath a globose body of cells (Pl. 13, figs. 5, 6). At higher magnifications it is clear that these cells are continuous with the vegetative hyphae (Pl. 13, fig. 6). Apparently the basal disc of radiating cells continues to enlarge to more than twice the diameter of the perithecium (Pl. 13; text-fig. 1). There is no evidence of hyphopodia on these radiating hyphae. The largest perithecium, presumably mature, although no spores were found within it, shows the lower portion of the perithecium and the numerous radiating hyphae (text-fig. 1). There are no setae or appendages of any kind on the lower portion of the perithecium. Unless they were present on the upper two-thirds of the perithecium, this species lacked any kind of mycelial or perithecial setae, an unusual feature in the Meliolaceae. Only the genus *Asteridiella* is without setae in the Meliolaceae (Hansford 1961). However, without complete perithecia it is not possible to place this fossil in an extant genus because some species of Meliolaceae have setae only on the perithecia (Hansford 1961). The fossil is best placed in the genus *Meliolinites* Selkirk. The stages of perithecial development in the fossil species are, so far as can be determined, the same as those in extant meliolas. Further collection and study should reveal additional stages of development as well as mature, whole perithecia.

The host leaves are fragmentary and oxidized, and are similar to leaves described by Ball (1931) and reported by Irving and Stuessy (1965) as *Nectandra*. In view of the estimate that up to 60% of the generic identifications made by early workers in the Eocene of south-eastern North America are incorrect (Dilcher 1973), the lauraceous affinities of the host leaves must be regarded as tentative at best. A detailed comparative study of the morphology and anatomy of the host leaves and modern lauraceous leaves will be required to provide a reliable identification. Hansford (1961) recognized forty-three species of meliolid fungi which parasitize lauraceous plants. None of these are similar to *M. dilcherii*.

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SOME ASPECTS OF COLONIALITY IN RUGOSE CORALS

by JERZY FEDOROWSKI

ABSTRACT. Early coloniality of *Heritschioides* sp. nov. from the Lower Permian (Upper Wolfcampian) of Texas has been studied in more than one thousand etched specimens. Ontogeny of the protocorallite differs from that of the only three known Devonian species. Septal insertion is initially of zaphrentoidal type. In early blastogeny the function of channels and *septal swellings* (new term) is of major importance. Division is thought to be an unimportant mode of reproduction and is associated with other modes, mainly lateral increase. The new term *lost structures* is introduced to describe offsets which are not capable of reaching maturity for some, probably genetic, reasons. They may appear in solitary as well as in colonial species, but are mainly associated with quasi-colonies. Capability to produce offsets should not be equated with maturity of an individual within the colony since this capability can be reached at different stages of individual development. Protopolyps and first asexually produced generations of polyps start to reproduce asexually earlier in ontogeny than polyps of astogenetically more advanced parts of colonies. The appearance of pseudo-offsets, pseudo-colonies, and composite colonies are regarded as being controlled at least in part by extrinsic factors.

PERMIAN rugose corals from south-western Texas have been studied most recently by Moore and Jeffords (1941), Ross and Ross (1962, 1963), and Fedorowski (1974). The large collection from this region belonging to the Department of Paleobiology, Smithsonian Institution is currently being studied by the present author, and this paper forms one part of that study dealing with some interesting aspects of coloniality.

The preservation of many silicified calices of corals in the collection is so perfect that certain characters of blastogeny, known previously only from serial sections, may be reinterpreted or made more precise. The interiors of other specimens are preserved partly in calcite, permitting the preparation of serial sections and acetate peels, and the results of this method were compared with the direct observations of calices. Excellent preservation of the material and the presence of specimens in different stages of astogeny (with protocorallites preserved) made a comparative palaeobiological study possible.

The precise systematic position of *Heritschioides* sp. nov. discussed here is not determined but will be described together with the remainder of the rugosans from south-western Texas in a separate paper. The stratigraphic position of the material is determined by Cooper and Grant (1972, locality USNM 728e) as being from the Bone Spring Formation of Upper Wolfcampian (Lower Permian) age.

ENVIRONMENTS

Environmental conditions discussed here are not based on field studies of sedimentology of the limestones, but observations on the corals themselves are introduced since they may add to previous environmental reconstructions (Stehli 1954) and, at the same time, aid in the understanding of some aspects of development and coloniality of the corals. I consider that all the specimens described belong to one species.

[Palaeontology, Vol. 21, Part 1, 1978, pp. 177–224, pls. 14–23.]

Dr. G. A. Cooper (*in litt.* 1974) writes that 'I think the corals probably belong to one population, but I would not say the same for the brachiopods'. All the specimens described here were etched from a few blocks of limestone coming from a single 60-cm thick bed (locality USNM 728e). However, according to both Dr. Cooper and Stehli (1954) the fauna of this limestone is redeposited. Stehli's (1954, p. 280) environmental reconstruction of the limestone is as follows:

> The bottom seems to have consisted of lime mud in which were embedded worn and broken shells and patches of shell sand. The deposit was not a reef but an area of somewhat quieter water marginal to a reef or shoal area offering a solid bottom.
>
> It is apparent that the deposit was formed in shallow water, but the exact depth cannot be determined. The worn shell debris and the position of the deposit, only 10 to 12 feet above an overlapped surface, all point to deposition in very shallow water.
>
> It is difficult to place the shore exactly during formation of this deposit, for the sea was advancing across a surface of generally low relief and the situation is secondarily complicated by post-Permian warping along the Victorio flexure. The shore seems to have been within a few miles, and probably islands dotted the inundated surface.
>
> An interesting feature of this and many other collecting localities is the complete imbalance of the organic assemblage. There are 10 times as many brachiopods as all others combined. Second in importance are the bryozoans which occur in large numbers, and include both stony forms and delicate fenestellids. Corals are present in moderate numbers.

The above reconstruction mainly concerns sedimentary conditions. It does not explain the primary living conditions of the fauna, although these conditions were most probably differentiated in spite of fact that all the skeletons were found in the same thanatocoenosis. The following short discussion on some characters of rugosans is introduced in order to show the importance of environmental influence in the development of colonies.

The microhabitats from which the corals came were differentiated as is indicated by the shape of corallites and colonies. Better-preserved samples may be grouped as follows:

1. Solitary corallites and protocorallites with strong talons (Pl. 15, figs. 10*b*, 13*a*; Pl. 16, figs. 6*b*, 8*b*; Pl. 17, fig. 1*a*; Pl. 21, fig. 6; Pl. 23, fig. 10*a*); colonies with attachment processes between corallites within the colonies and with large surfaces of attachment at the beginning of astogeny (Pl. 16, fig. 4*c*; Pl. 18, fig. 1; Pl. 20, fig. 5). All these corals were attached to a hard matrix, and may indicate a rocky bottom in a zone of wave activity or in an area affected by currents. One or two of the circumrotary colonies found in the collection (Pl. 21, fig. 1*a–d*) also belong to the group growing on a rocky or hard sandy bottom, as this was the only possibility for them to survive. They possess corallites growing in all directions and were probably overturned a few times without having been killed.

2. Quasi-colonies with no strong talons (Pl. 19, fig. 7*a*; Pl. 21, figs. 8, 9); weakly fasciculate colonies with no attachments between particular corallites (Pl. 17, fig. 7); small colonies in which only protocorallites were attached to the substrate (Pl. 16, figs. 2, 5, 7); and colonies consisting of long, parallel corallites (Pl. 21, fig. 11). Corals of this group form a majority in the collection, but most are preserved only as fragments. Lack of talons and other attachment processes indicates that they were inhabitants of rather quiet areas on a lime sandy bottom. Their habitats were not necessarily far from those of the first group, however.

3. The third group is an intermediate group. The following types of specimens can be included: corallites and small colonies attached to the internal parts of brachiopod shells, to fragments of corals or to other comparatively large fragments of debris (Pl. 15, fig. 6; Pl. 21, figs. 3–7; Pl. 23, figs. 1*b*, 2, 3); colonies of corallites packed closely to each other, but with no interconnecting processes (Pl. 17, figs. 6, 8; Pl. 21, fig. 4), and chain-like colonies (Pl. 18, fig. 3*a*, *b*). These specimens came from a bottom covered by larger fractions of calcareous sand and organic fragments offering many opportunities for larvae to settle.

Some other observed phenomena may also be connected with either the first or third group. Some colonies rapidly changed their direction of growth without being detached from the bottom (Pl. 17, figs. 1*a–d*, 4*a–b*), or grew only in one direction (Pl. 17, figs. 3, 5*a–b*). This must be related to currents and to rapid changes in their directions. Other corallites show many rejuvenescences and deep narrowings (Pl. 17, fig. 1*c*; Pl. 20, figs. 4*a–b*; Pl. 22, figs. 2, 10*a–b*) which are also related to environmental changes.

The three groups of corals listed above do not differ in internal morphology of corallites or in blastogeny. There are no strong boundaries between them and many corallites show intermediate characters indicating that there were no sharp boundaries between habitats. Their primary living area was probably a shoal, differentiated in morphology, with prevailing wide sandy areas colonized by the second group. There were also rocky, underwater dividing ridges with corals of the first group attached to them, and patches of coarse-grained lime sands inhabited by members of the third group. Local currents flowed at different velocities and in various directions. Waves might have swept the more elevated areas. These habitats may be compared with the coralgal lithofacies of Bathurst (1975).

There is little to add to Stehli's (1954) reconstruction as far as sedimentary conditions are concerned. Transportation of the material definitely took place, but not over a great distance and not along the sea-shore, as there is no evidence of rounding. The material was not segregated by current action. All three groups of corals in all astogenetic stages, as well as solitary corals, have been found together.

Such a mixture of ecologically and astogenetically different specimens was most probably caused by a common factor acting simultaneously in all areas where the corals lived. Storms with deep waves may have been important, as they might have affected all areas simultaneously. This is in agreement with observations by Ball *et al.* (1967) on recent sedimentary conditions on the Bahama Bank. The uprooted specimens and their broken fragments were mixed and partly crushed during transportation through the shallow water towards the sea-shore, but were deposited before reaching it. Dr. G. A. Cooper (*in litt.*) suggests that 'sedimentation was rapid', and this interpretation is certainly supported by the coral fauna. There is thus no reason not to consider the whole collection as belonging to a single population.

TERMINOLOGY

All terms are new unless noted to the contrary. My interpretation of some old terms may differ to some extent from previous meanings.

Channels (Fedorowski and Jull 1976)—openings between a parent and daughter corallite covered by a common parent/offset soft tissue.

bridged channels—openings as above, but bridged by a partition.

Colonies

composite colony (Oliver 1968)—a colony that was initiated by more than one protopolyp. Particular corallites may grow close to one another but their soft tissues are not united.

incipient colony (Fedorowski 1970)—a superindividual in which a parent corallite is the only mature corallite. Offsets produced in peripheral increase do not reach maturity for combined genetic and environmental reasons.

pseudo-colony (Fedorowski 1971, not in the sense of Spassky and Kravtsov 1974)—a cluster of individual corallites of the same species that grow close to one another, giving the impression of being produced by offsetting.

quasi-colony (Fagerstrom and Eisele 1966)—a superindividual in which a parent corallite is the only mature corallite. Offsets are *lost structures* (see below).

Division (widely used term)—characterized by the entire parent corallite being divided into two more or less equal descendent individuals.

offsetting-like division—a parent corallite is an easily recognizable specimen.

twins—a double-calice offset that looks like a corallite which is incompletely divided.

Lost structure—an offset produced in lateral increase that did not reach maturity for reasons other than environmental ones (probably genetic).

Pseudo-offset—a corallite that starts to grow in the calice of a dead specimen of the same species, giving the impression of being offset.

Rejuvenescence (widely used term)—an action of a polyp leading to reduction of dimensions by leaving part of some skeletal structures in a calice outside a new external wall.

axial rejuvenescence—a polyp retained in the middle part of its old calice, leaving peripheral parts outside its new external wall.

lateral rejuvenescence—a polyp leaves a large part of the periphery of its old calice outside its new external wall, but continues to develop all previous structures in the rest of its calice.

shallow rejuvenescence—closely comparable with deep narrowings of growth, but in contrast to them the new and old external walls are separated.

Septal pinnacles (Fedorowski and Jull 1976)—upper tips of internal parts of septa in a region of increase that continues to grow upwards. In cross-section they appear to be separated from *septal swellings* (see below) cue to cessation of growth of the latter.

Septal swellings—upgrowths of upper margins of septa in a region of increase.

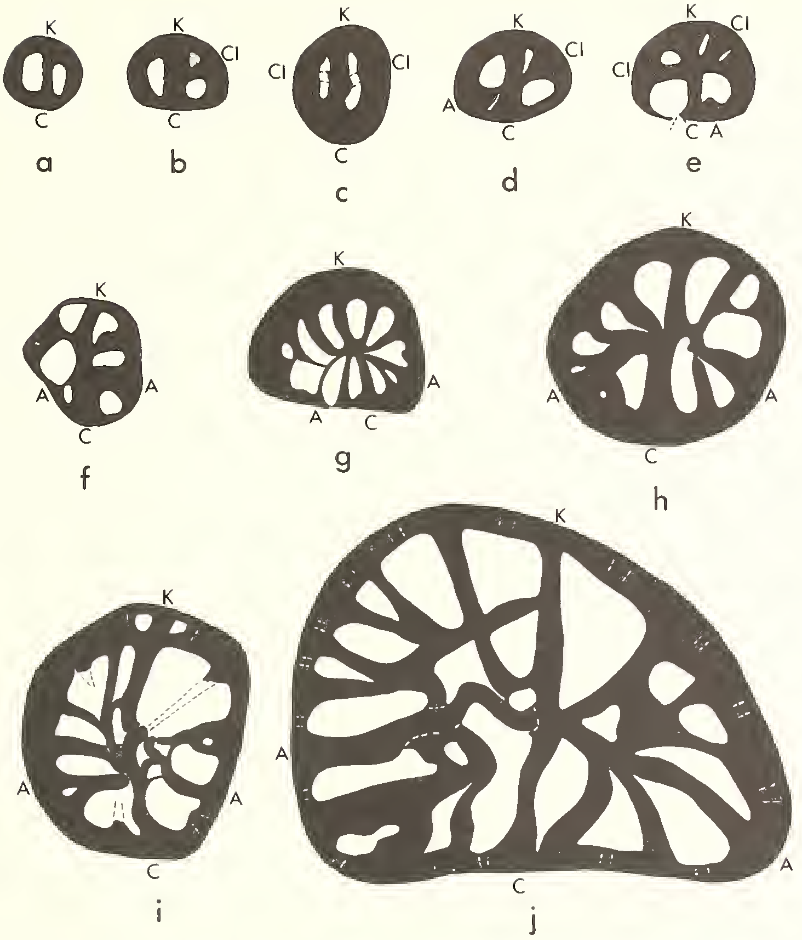
bounding septal swellings—structures that bound a region of increase and may be converted into new septa of a parent and a daughter corallite.

inside septal swellings—structures retained in a daughter corallite as main supporting elements of the base of its calice.

For other terms concerning blastogeny see Hill (1956) and Fedorowski and Jull (1976).

ONTOGENY OF THE PROTOCORALLITE

All important stages of development and septal insertion, beginning with a very young brephic stage of approximately 0·75 mm diameter, possessing only one axial septum, were available for study (text-fig. 1). No aseptal, tube-like stage was observed directly, but well-preserved axial ends of some specimens suggest that the initial part of the protocorallite may have been a cup-like structure with no skeleton except for the external wall. That cup was later filled by sclerenchyme deposited by the basal ectoderm. Such solidly sclerenchymal tips were observed in quite a few corallites. It seems probable that the axial septum was inserted early, both on the basal disc and simultaneously on the wall in a common fold of the ectoderm. This type of development is a little different from that described by earlier workers in the only known protocorallites of three Devonian species. These are the Middle Devonian *Hexagonaria anna* (Whitfield) from Michigan studied by Stumm (1967) and Jull (1973),



TEXT-FIG. 1. Camera-lucida drawings of young ontogenetic stages of protocorallites. C—cardinal septum; K—counter septum; A—alar septa; Cl—counter-lateral septa (indicated only when not obvious). All figs. × 15.

a–f—brephic stage. *a*, USNM 196565, early brephic stage with an axial septum; *b*, USNM 196566, a counter-lateral septum is inserted next after axial septum; *c*, USNM 196567, probable existence of two counter-laterals prior to the alars; *d*, USNM 196568, one counter-lateral and one alar are the only recognizable lateral protosepta; *e*, USNM 196570, existence of only one alar septum is certain; a first metaseptum is inserted in counter quadrant; *f*, USNM 196569, six well developed protosepta.

g, *h*—neanic stage; arrangement of septa zaphrentoidal; axial septum invariably present; an acceleration of septal insertion in counter quadrants; an irregular insertion of initials of minor septa; *g*, USNM 196571; *h*, USNM 196572.

i, *j*—late neanic stage; an axial septum is often divided into cardinal and counter septa; some septa, mainly protosepta, become elongated to form an axial structure; recognizable minor septa are definitely present; *i*, USNM 196573; *j*, USNM 196574.

and the Upper Givetian *Phillipsastraea hennahi* (Lonsdale) and *H. philomena* Glinski from Nakhichevanska S.S.R. studied by Ulitina (1973, 1974). All these species show a definite aseptal, tube-like initial stage of growth and the further insertion of septa different from that described below.

Brephic stage. Counter-lateral protosepta appear to be inserted as the next protosepta after the axial septum; their insertion may have been in sequence rather than together. The structure shown in text-fig. 1*b* may be the beginning of the first counter-lateral septum. The growth stage at diameter 0·9 × 1·6 mm (text-fig. 1*c*) appears to possess both counter-lateral septa, although they are not sufficiently distinct to be distinguished with certainty. The insertion of protosepta after the axial septum may be quite irregular. Text-fig. 1*d* shows an example in which only one alar and one counter-lateral septum can be distinguished, and text-fig. 1*e* shows insertion of a first metaseptum in the counter quadrant, although only one alar protoseptum can be barely distinguished. Text-fig. 1*f* is an example of a regularly developed later brephic stage with axial septum, and with regularly arranged alar and counter-lateral septa.

Wetted surfaces of some corallites show several septal lines on the outer surfaces of the walls with no comparable septal structures penetrating the interiors of the protocorallites. These lines may indicate very fast insertion of initial stages of septa. Some of them may be minor septa. The septal lines which definitely belong to minor septa adjacent to the cardinal septum begin a little later in growth, and can easily be seen as lines joined with the cardinal septum line and continued to the uppermost part of the corallite. Insertion of other septa, which can be determined as certainly as the minors, seems to be irregular.

Neanic stage. No step-by-step description of this stage of development is made here as it seems to be normal for the suborder Streptelasmatina and as such is reasonably well known. The following features may be characteristic of the species under discussion or, possibly the genus. Some of them are discussed as individual variation.

1. In most calices, and on the broken proximal ends of observed protocorallites, there is a small but distinct acceleration of septal insertion in the counter quadrants. This may be quite variable in the early neanic stage, when acceleration of septal insertion in only one of the counter quadrants can be observed (text-fig. 1*h*), but seems to be regular later. More or less equal numbers of septa in all quadrants in the early neanic stage is very uncommon.

2. The arrangement of septa is zaphrentoidal (text-fig. 1*g*, *h*), but they may be deformed because of flattening of the side of the corallite attached to the substrate. As a rule this is on the cardinal septum side. In the earlier part of this stage cardinal and counter septa are still joined, producing a regular axial septum to which the alar and counter-lateral protosepta are connected. In Plate 15, fig. 1*a*, *b* two phenomena are shown that may increase the understanding of calices as studied in transverse section: (*a*) the zaphrentoidal arrangement of the septa is more or less clear only on the bottom of the calice, while the arrangement of septa on the walls is almost radial, with the last pairs of metasepta slightly underdeveloped; (*b*) there is a distinct pseudocolumella in the centre of the calice, while in the comparable transverse section of the base of the calice only the connected cardinal and counter septa are visible. The cardinal septum is depressed before its junction with the axial lamella, which indicates the existence of a cardinal fossula.

3. During the early neanic stage the cardinal and counter protosepta of some corallites become separated. An important step in phylogeny takes place after separation, in that the cardinal septum remains elongate and the axial structure is built around its axial end. There is a general tendency for all the axial lamellae or axial ends of septa within the species to curve around the axial structure. The cardinal protoseptum and its axial lamella remain straight for a longer period than other septa or lamellae.

4. The construction of the axial structure may be variable and is heterochronic in most observed cases. Some small (approx. 3 mm diameter) specimens possess a kind of loose axial structure and separated cardinal and counter protosepta (text-fig. 1*i*) whereas other specimens which are almost twice as large (text-fig. 1*j*) retain the axial septum. Most commonly the axial structure is built with the axial lamellae joined to the axial ends of the septa just above the bottom of the calice, and with elevated axial tabellae. The axial structure of more advanced stages observed both in calices and in transverse sections just beneath the calices show a network of septal lamellae and axial tabellae. The cardinal protoseptum may be located in a narrow cardinal fossula, but it remains connected with its axial lamella along the bottom of the fossula.

BLASTOGENY

Lateral increase

Origin and function of more important structures. Septal swellings are the structural elements that originate directly from the upper peripheral margins of a few septa of the parent corallite (Pl. 14, figs. 2, 3*a*). These septa, located in a region of increase, stop to grow upwards and become grossly thickened by stereoplasmatic sheets to strengthen their mechanical resistance (Pl. 14, fig. 3*b*). Such a rearrangement of construction is conditioned by their new character, position, and function. Retaining fine septal structure they become converted into the main basal skeletal elements of an offset (Pl. 14, figs. 4*a*, 5*a*, 10). Their second important function is to border channels (Pl. 14, figs. 3*b*, 5*a*).

Situated more inwards towards a calice of the parent corallite, and directly united with septal swellings, are other skeletal elements that also originate from the upper margins of septa. These are *septal pinnacles*. In contrast to septal swellings they grow consistently upwards, preserving their character as vertical skeletal elements. Although they appear to be separated when observed in cross-sections made above septal swellings (Fedorowski and Jull 1976, text-fig. 3), they are in fact directly connected with the upper margins of septa (Fedorowski and Jull 1976, text-fig. 1; Pl. 14, figs. 4*a*, 5*b* herein). The etched septal pinnacles with new septa being formed on them are shown on Plate 14, fig. 5*a*–*b* to illustrate the relationship of parent septa, septal swellings, septal pinnacles, and new septa of an offset.

Interpretation of *channels* (Fedorowski and Jull 1976) based on serial sections can be supplemented by observations made on etched material. Channels were initiated simultaneously with septal swellings, are always located between them, and are ditch-like at their initial stage (Pl. 14, fig. 5*b*). Further development begins at the same time as the formation of new septa on the tips of septal pinnacles. These new septa are quickly and distinctly thickened, tending to meet each other above the channels (Pl. 14, fig. 5*a*). Growing both vertically and laterally they soon form a solid partition which bridges the channels close to the parent polyp. These bridged channels are surrounded by skeletal structures extending continuously between parent and offset calices (Pl. 14, fig. 5*a*; Pl. 16, figs. 10*c*, 11). Such common structures must have been covered by a common soft tissue that connected the parent and the offset polyps.

The existence of tabellae, dissepiments, etc., between septal swellings in the common parent/offset area, and inside the youngest parts of offsets investigated in serial sections led to the earlier interpretation of channels and of the period of their activity. These structures are all secondary, i.e. were all built some time after the existence of open, bridged channels. An example of a young corallite completely separated from its parent corallite by a dividing wall, but connected to it by the channels is shown on Plate 22, fig. 6*a–c*. It seems clear that the soft tissues of these two polyps were united along the walls of the channels. On the other hand, however, there are examples of

EXPLANATION OF PLATE 14

Fig. 1. USNM 196575, ×2. False region of increase on widened shoulder of calyx; *a*, calicular view; *b*, side view.

Fig. 2. USNM 196576, ×2. A very beginning stage of blastogeny. Minor septa become contratingent to the majors.

Fig. 3. USNM 196577, ×6. *a*, hystero-brephic stage a little more advanced than illustrated in fig. 2. Septa only start to transform into septal swellings; *b*, another offset of the same colony showing well developed septal swellings, with septal pinnacles starting to bridge channels.

Fig. 4. USNM 196578, ×6. *a*, hystero-brephic stage with distinct, smooth septal pinnacles, common for major and minor septa of a parent corallite; *b*, another offset of the same colony with channels and with initials of septa on septal swellings in a calyx of offset.

Fig. 5. USNM 196579. *a*, two neighbouring offsets in hystero-brephic (*left*) and hystero-neanic (*right*) stages. Differentiation in speed of development of inside and outside parts of an offset is well illustrated by the right offset. It also shows a secondary folding of septal swellings, converting them back into septa, ×6; *b*, structure of a septal pinnacle, ×12.

Fig. 6. USNM 196580, ×6. Early hystero-neanic stage with axial septum present.

Fig. 7. USNM 196581, ×6. Hystero-neanic stage with septa differentiated in length, but with no pseudocolumella. Traces of channels are still distinguishable.

Fig. 8. USNM 196582, ×6. Hystero-neanic stage with beginning of a pseudocolumella.

Fig. 9. USNM 196583, ×6. Two offsets belonging to different parents, as it is indicated by remainders of channels in the left offset.

Fig. 10. USNM 196584, ×6. Hystero-neanic stage. Beginning of development of axial structures, resulting from junction of axial ends of some septa.

Fig. 11. USNM 196585, ×4. Hystero-neanic stage.

Fig. 12. USNM 196586, ×6. Channel in lateral view.

Fig. 13. USNM 196587, ×6. Hystero-neanic stage. A thick, solid partition and insertion of septa close to an external wall. Pseudocolumella delayed in development.

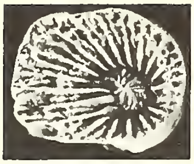
Fig. 14. USNM 196588, ×4. Early ephebic stage with dividing wall developed, but with an axial septum, instead of pseudocolumella, still present.

Fig. 15. USNM 196589, ×6. Late neanic stage. Beginning of development of axial structures.

Fig. 16. USNM 196590, ×4. Late neanic stage. Four almost simultaneous offsets with well-developed axial structures.

Fig. 17. USNM 196591, ×4. A shallow rejuvenescence. Major septa are continued from the old to the new part of calice.

PLATE 14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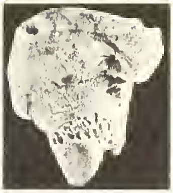
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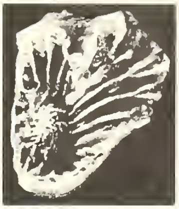
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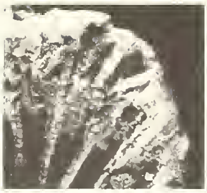
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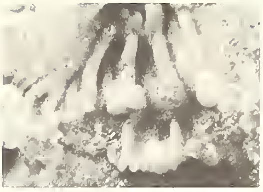
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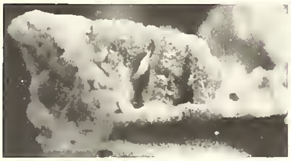
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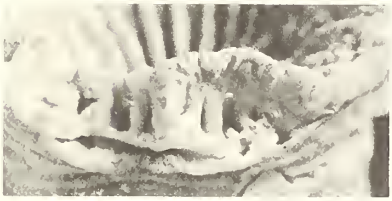
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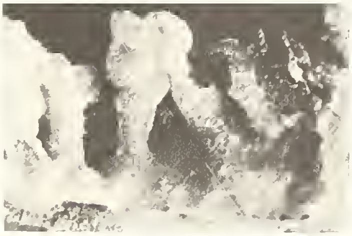
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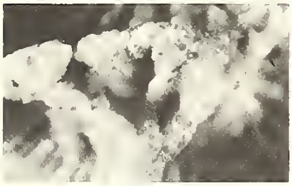
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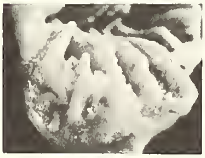
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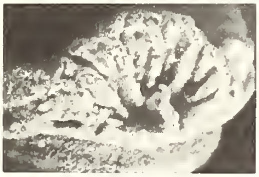
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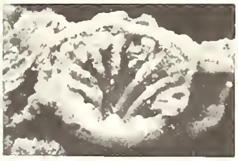
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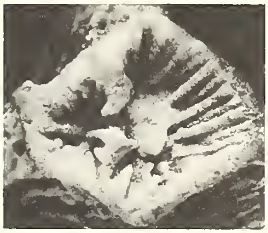
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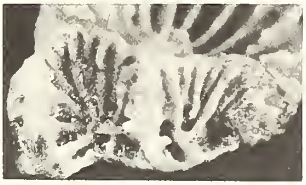
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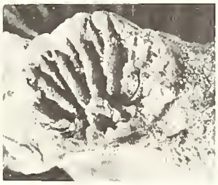
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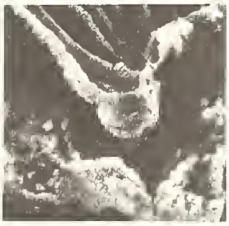
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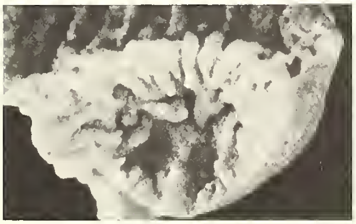
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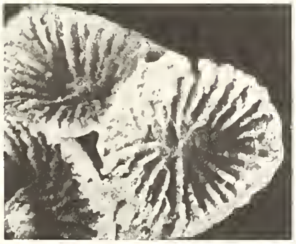
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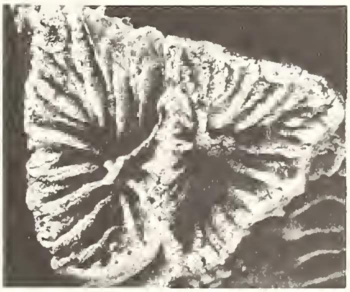
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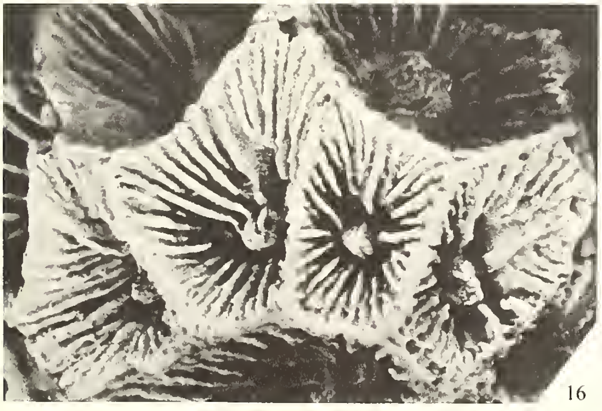
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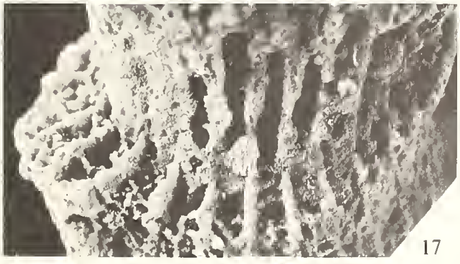
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FEDOROWSKI, coloniality in rugose cotals quite young corallites that were cut off from the parent corallite, mainly or exclusively by the action of the parent polyp. These are lost structures (Pl. 23, figs. 7, 11).

The process of disjunction of an offset and parent in channels is slow and develops step-by-step (Pl. 22, figs. 5, 6*c*; text-fig. 2A). Dissepiments are the main structural elements overgrowing the bridged channels. The direction of construction of particular dissepiments on the parent corallite side is centripetal. The newly constructed dissepiments in channels are convex towards the parent calice, when constructed on its side. The observed direction of appearance of dissepiments indicates that the uppermost row meets the upper margin of the bridged channel (Pl. 22, fig. 6*c*). The soft tissue must have covered both of these elements in contact. The supposition that it had atrophied along the line of contact seems to be the only possible explanation for the disjunction of the parent and offset polyps. The separated bodies were sealed over and continued to grow separately.

The overgrown channels are distinguishable for quite a long period of development in a parent corallite calice. They are marked by an apparent interruption of minor septa (Pl. 22, fig. 5). This 'interruption' is caused by a characteristic development of septal pinnacles and by the origin of partition. Two major septa, which bound particular channels, are continuously secreted on septal pinnacles and there is no major change in their structure either during the existence of open channels (Pl. 16, fig. 11; Pl. 22, fig. 6*c*) or when the channels are overgrown (Pl. 22, fig. 5). The situation of minor septa is different, as they are located in the loculi occupied by channels. They cease development at the point when channels begin to form (text-fig. 2A, position s_1 of septum) and their growth is not continued during the whole period of activity of open channels. However, when partition takes place septal structures appear between the major septa, exactly in the same loculi where the former minor

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EXPLANATION OF PLATE 15

All figs. ×4.

Fig. 1. USNM 196592. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.

Fig. 2. USNM 196593. Calicular view of non-offsetting protocorallite.

Fig. 3. USNM 196594. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.

Fig. 4. USNM 196595. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.

Fig. 5. USNM 196596. Non-offsetting protocorallite. *a*, calicular view with well developed axial structure; *b*, side view.

Fig. 6. USNM 196597. Non-offsetting protocorallite attached to inside of brachiopod shell.

Fig. 7. USNM 196598. Non-offsetting protocorallite. *a*, calicular view; *b*, side view.

Fig. 8. USNM 196580. Protocorallite with first offset (see also Pl. 14, fig. 6). *a*, calicular view; *b*, side view of a very irregular shape.

Fig. 9. USNM 196599. Protocorallite with first offset. *a*, calicular view; *b*, side view.

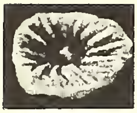
Fig. 10. USNM 196600. Protocorallite with first two offsets produced early in ontogeny. Strong attachment to a bryozoan colony. *a*, calicular view with second offset; *b*, side view with first offset.

Fig. 11. USNM 196601. Protocorallite with first offset. *a*, calicular view; *b*, side view.

Fig. 12. USNM 196602. Protocorallite with two almost simultaneous offsets. *a*, side view; *b*, calicular view.

Fig. 13. USNM 196603. Protocorallite with three first offsets. *a*, side view; *b*, calicular view.

Fig. 14. USNM 196581. Calicular view of protocorallite with three first offsets (see also Pl. 14, fig. 7 and Pl. 23, fig. 7).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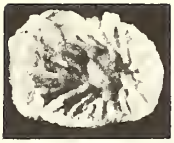
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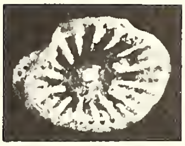
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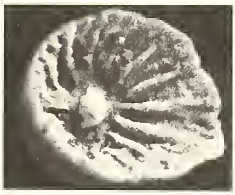
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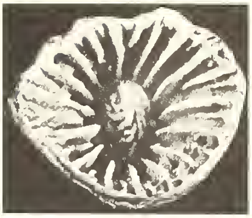
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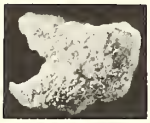
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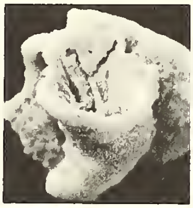
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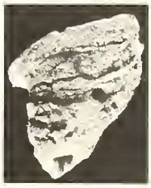
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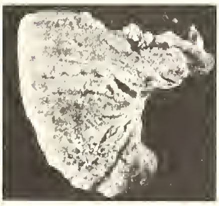
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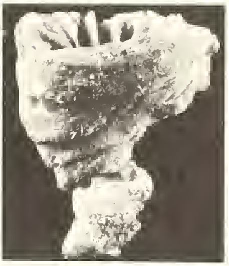
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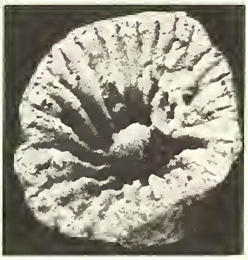
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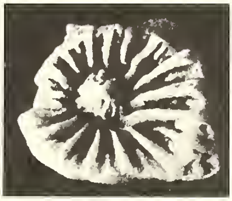
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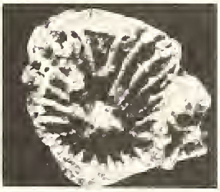
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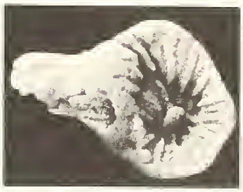
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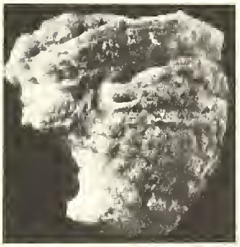
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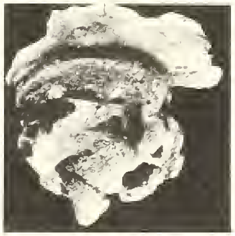
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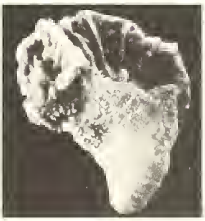
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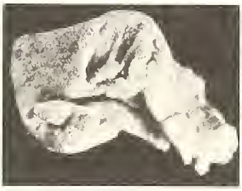
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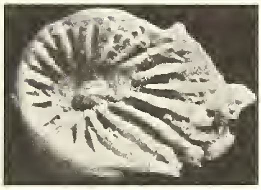
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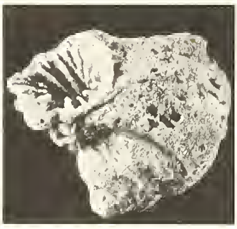
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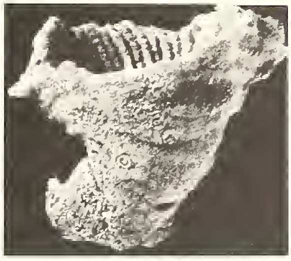
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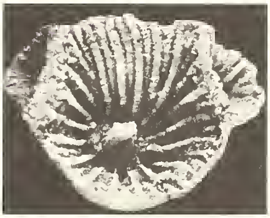
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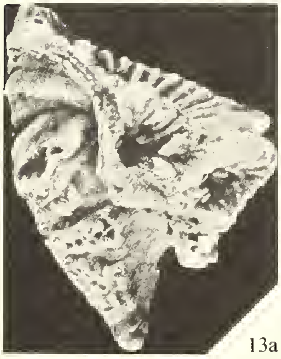
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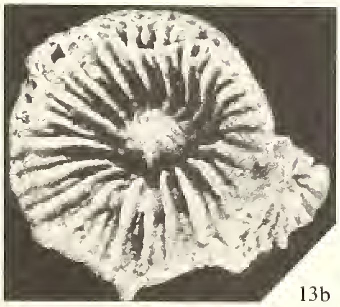
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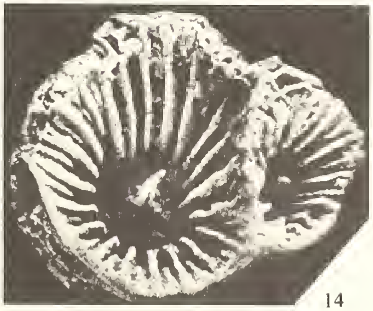
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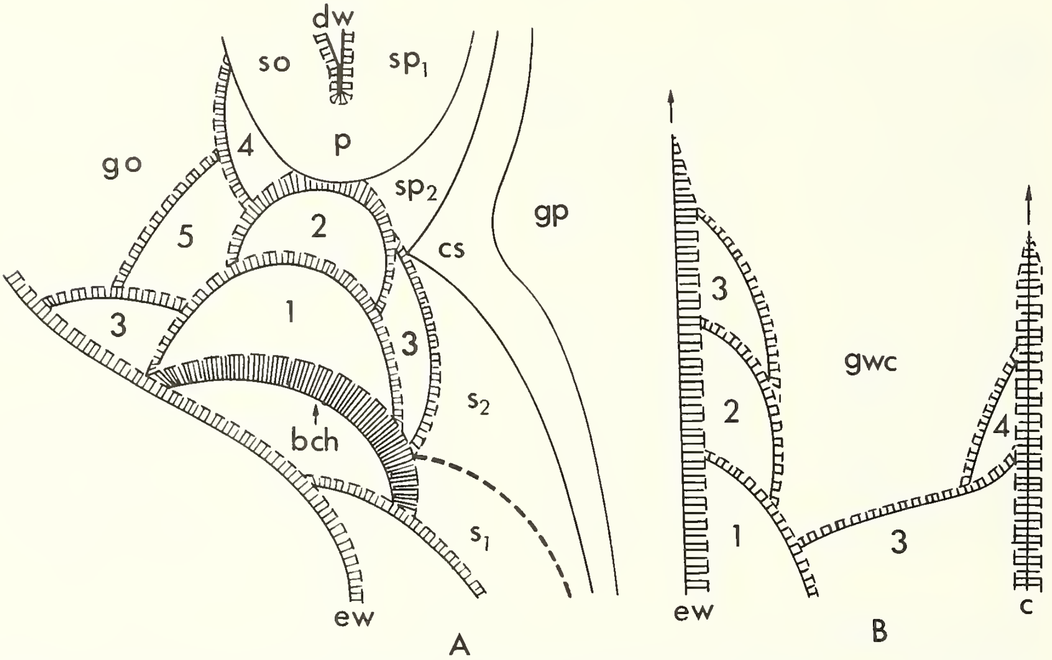
FEDOROWSKI, coloniality in rugose corals

septa were located (text-fig. 2A, position sp_1; Pl. 16, figs. 10*c*, 11). Shortly after the channels are overgrown by dissepiments the old minor septa start to grow upward, based on surfaces of these dissepiments (text-fig. 2A, position s_2). It is also probable that the new minor septa, which appeared on partition, start to develop downwards and inwards in the calice as soon as the bodies of parent and offset polyps are separated (text-fig. 2A, position sp_2). A seeming interruption of minor septa is especially well expressed in this stage of development (Pl. 22, figs. 5, 6*c*—loculum 4). In further growth of a parent corallite, septal invaginations of the ectoderm of a parent polyp in which the parts of the minor septa mentioned above are secreted become united. Starting from this point there is no trace of channels in the skeleton of a parent calice, and only continuous minor septa are seen (text-fig. 2A, position cs).



TEXT-FIG. 2. A, reconstruction of overgrowth of channel, based in part on Plate 14, fig. 12 and Plate 22, figs. 5, 6*c*. Not to scale. B, appearance of particular structural elements in calice. Permanently upward-growing structures are indicated by arrows.

1–5—sequence of appearance of particular basal structural elements; bch—bottom of channel; c—pseudocolumella; cs—continuous minor septum; dw—dividing wall; ew—external wall; go—gastro-vascular cavity of offset; gp—gastro-vascular cavity of parent; gwc—gastro-vascular cavity; p—partition; s_1, s_2—positions of old minor septum before and after the channel was overgrown; so—new minor septum of offset; sp_1, sp_2—positions of new minor septum of parent before and after the channel was overgrown.

Because of technical difficulties all the processes which took place in channels were observed only from the side of the parent corallite. Judging from the depth of channels in the offsets they became overgrown here later than on the parent side. Observations in serial sections show that this too was a step-by-step process. Dissepiment-like or tabula-like basal plates were built one after another between septal swellings as soon as the soft tissues of the parent and daughter polyps became separated.

The channels in most of the corallites studied are in pairs. This may have had some functional importance as the pair of channels would enable a flowing liquid to be divided into two currents—from the gastral cavity of a parent polyp through one channel and back through the other. This would make the currents more effective, as the food- and oxygen-bearing water would not be mixed with that from which the food and oxygen were already extracted. This is a rather speculative conception and it is also possible that water was pumped either by the parent polyp to the gastral cavity of the daughter or vice versa in one direction only. Of more importance than water supply seems to be the direct connection of soft tissues of these two polyps. This would enable the parent polyp to provide an offset directly with any required substances. These dual functions of the channels were especially important in the early stage of blastogeny when tentacles of the young polyp were either absent or underdeveloped, and the capability of the young polyp to grow independently was rather low. The lost structures, discussed below, may have resulted from premature separations of offsets.

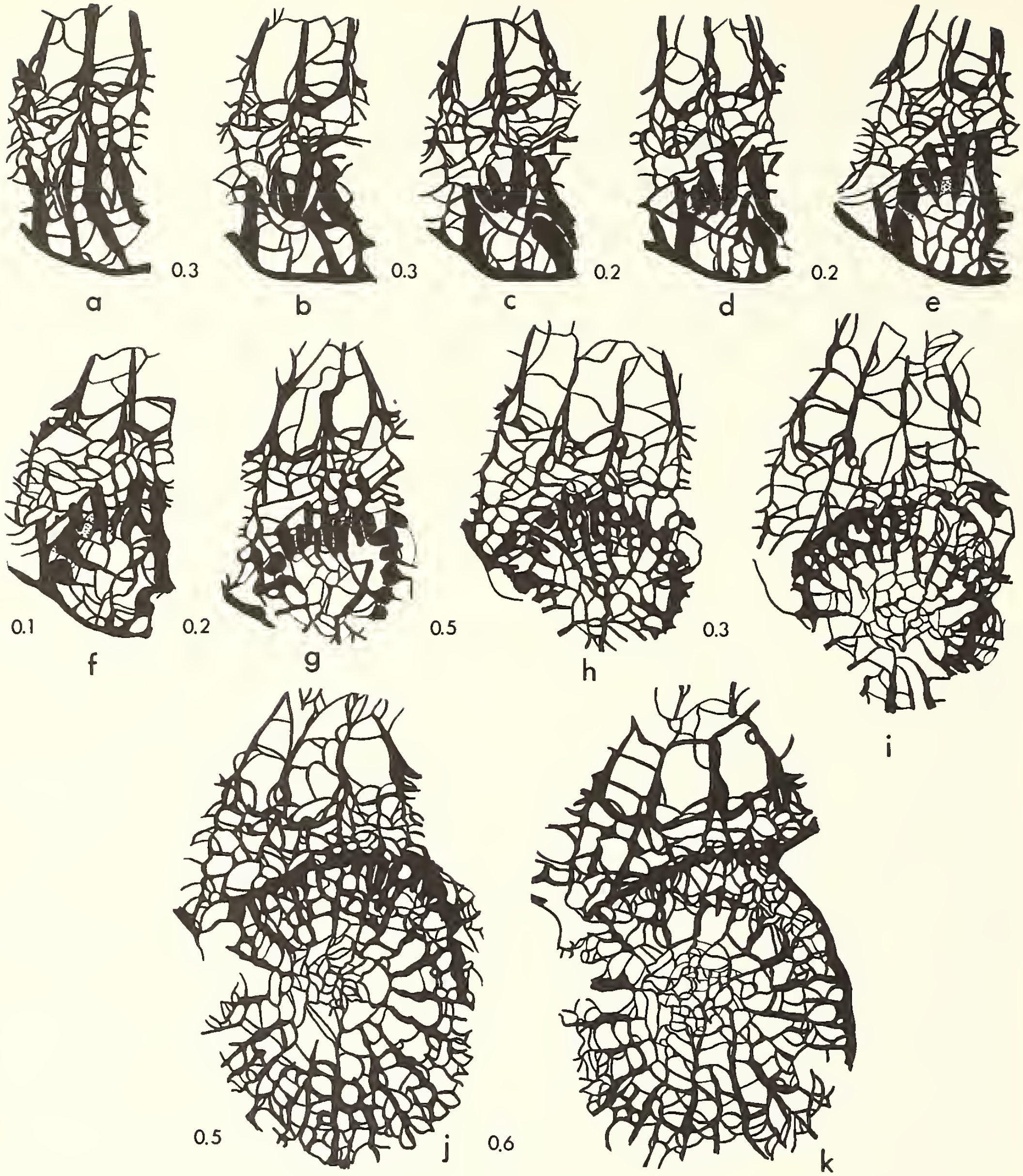
Serial sections. Blastogeny begins with the appearance of four septal swellings (text-fig. 3*a*), two of which bound the region of increase and two others develop inside it. The dissepimental tissue remains continuously dense there, although it may be irregular in places (text-fig. 3*a*).

One of the two inside septal swellings is divided into a peripheral offset septum and a pinnacle. The pinnacle is simultaneously split to form bases for two future septa. The second inside septal swelling remains complete in the central area of the offset and initiates an axial structure. The septal pinnacle is separated from its inner area (text-fig. 3*b*).

After approximately 1 mm of growth of the offset one of the bounding septal swellings is replaced by two or slightly more new, thick septa, and the same happens with the second swelling after a further 0·3 mm growth (text-fig. 3*e*, *g*). This replacement takes place on the upper margin of the bounding septal swellings, where the ectoderm became secondarily folded. The new septa have a dual function initially since they also form a solid partition, a bounding element, which functionally replaces bounding septal swellings (text-fig. 3*g*, *i*).

Approximately contemporary with the rearrangement of the structure of the bounding septal swellings, new septa appear in the common parent/offset area (text-fig. 3*g*). They are always closely connected with the septal pinnacles, being developed on the tips of them. Their function, as with those originating from bounding septal swellings, is twofold, both septal and bounding, since they form a solid partition connected directly with the partition built of the transformed bounding septal swellings (text-fig. 3*i*, *k*).

Septal insertion is irregular and differs from the regular zaphrentoidal insertion observed in protocorallites. This results from the very rapid transformation of the bounding septal swellings into septa, and the almost simultaneous appearance of new septa on the tips of pinnacles. Only on the peripheral wall of the offset are a few new septa inserted slowly (text-fig. 3*d*, *e*). Their sequence of appearance suggests that the



TEXT-FIG. 3. Lateral increase of USNM 196669 in serial sections. All figs. ×7.

a, *b*, hystero-brephic stage with septal swellings (*a*) and long septal pinnacles (*b*). Cardinal septum is the only inherited septum. It becomes a base for an axial structure of the offset.

c–g, hystero-neanic stage with almost no insertion of septa during first 0·8 mm of growth (*c–f*) and with rapid insertion during next 0·2 mm (*g*). The bounding septal swellings are divided into two (*e*, left swelling) or many (*g*, right swelling) new septa. A partition is first built of septal pinnacles (*c–f*) and then of new septa (*g*).

h–j, neanic stage. Does not differ in structure from that of a protocorallite, except for a little more irregular arrangement of structural elements near the partition.

k, late neanic stage with partition still present, but with dividing wall simultaneously built from both sides of a common parent/offset area.

septum from which the pseudocolumella is built is the cardinal septum, and that this septum is inherited, located on the peripheral wall.

From its origin an axial structure (text-fig. 3*c*, *d*) is built around the axial end of one septum, but there is at least a short period of growth with a continuous medial plate (text-fig. 3*b*). Septal lamellae are irregular, curved, and may be distinguished from axial tabellae only by their fine structure.

Observations on calices and comparison with serial sections. The following discussion is based on a summary of observations made on many calices of offsets of different colonies. The beginning of blastogeny is marked by the rearrangement of structures of the shoulder of the calice, a part of which becomes wider and flatter (Pl. 14, figs. 2, 3*a*). This limited region is the only part of a corallite subject to changes due to increase. Most of the parent calice remains unchanged (Pl. 15, figs. 8*a*, 9*a*, 10*a*). The flattening itself is not indicative of the beginning of offsetting, as there are many deformations of calices related to attachment processes, etc. (Pl. 14, fig. 1*a*, *b*). A flattened calice caused by extrinsic factors may be distinguished from one at the beginning of offsetting in not having differentiated septa.

Growth of a new individual, in all observed cases, is initially directed inwards towards the calice of the parent corallite. Such a young offset is completely within and protected by that calice (Pl. 14, figs. 3*b*, 5*a*). This early hystero-brephic stage has a shelf-like shape and possesses two septal swellings as the only structural elements (Pl. 14, figs. 3*a*, 5*a*). During further growth of an offset, septal pinnacles are developed as supporting elements in the common parent/offset area (Pl. 14, figs. 3*b*, 4*a*, 5*b*). Their secondary folding to form the initial stages of new septa may be fairly clearly observed (Pl. 14, figs. 3*b*, 4*b*, 5*a*). These new septa develop quickly and expand laterally to form a solid partition and to bridge channels (Pl. 14, figs. 8, 10, 11, 13; Pl. 16, fig. 11).

The morphology described above differs from that of the hystero-brephic and hystero-neanic stages discussed earlier in the account of serial sections. There are no basal structural elements in the calices, while in sections many dissepiments and/or other basal plates are present between the septal swellings. The origin of these phenomena is discussed earlier in connection with channels.

A further aspect regarding development as seen in both calices and serial sections involves different rates of development of particular regions of offsets. In many examples (e.g. Pl. 14, figs. 7, 8, 10, 11) the inner regions of a young individual, close to the parent corallite, are generally higher, often significantly, than their outer regions. The inner regions are also more advanced in morphologic development, and in particular have many more septa. Only a few septa, mostly inherited, occur in the outer region of a young offset. The very rapid growth of the common parent/offset area is most probably caused by atrophism of a new polyp tending to deflect from the parent corallite. This may be explained by a need to occupy a water space which is not exploited by the parent polyp. These differences of speed of development of particular parts of the calice cause the internal structure of young corallites to be differentiated when observed in serial sections. Different parts of the same section (outer and inner) belong in fact to different stages of development since they were secreted at different times.

As in the ontogeny of protocorallites, but less clearly so, the arrangement of septa in young calices of offsets is zaphrentoidal. This can be established mainly by observation of the position of incompletely developed septa on the walls of calices (Pl. 14, figs. 7, 8, 10, 14). With further development this arrangement is modified by the appearance of basal elements and an axial structure, as seen in transverse serial sections.

The pseudocolumella is distinguished very early in most of the corallites examined. It is commonly connected to two septa orientated perpendicular to the partition between parent and daughter corallites. One of these two septa, commonly the peripheral (cardinal) septum dominates, while the counter septum, although connected directly to the pseudocolumella, is visibly not as prominent as the other. The fine structure of pseudocolumellae may be either monoseptal or biseptal. None of the axial ends of septa or septal lamellae are incorporated into it, although it may resemble a compound pseudocolumella (Pl. 14, fig. 16).

There is a rather distinct variability within young corallites in their shape and dimensions, speed of growth, appearance and differentiation of particular structures, etc. Most variations are not important as they are either small changes or appear within one colony and, as such, are somatic and may have been environmentally controlled. The positions of cardinal and counter septa appear to be of primary importance. In most observed corallites the cardinal septum is situated at the external wall of the offset and is inherited from the parent corallite. In four or five small colonies the situation is reversed, and in these cases the counter septum is the basic septum for the axial structure. Unfortunately all these colonies are at an initial stage

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EXPLANATION OF PLATE 16

Fig. 1. USNM 196604, ×2. Protocorallite with two offsets arranged symmetrically due to attachment. *a*, calicular view; *b*, side view.

Fig. 2. USNM 196605, ×2. Protocorallite with four offsets arranged asymmetrically, all on one side. *a*, calicular view; *b*, side view.

Fig. 3. USNM 196606, ×2. A first asexually produced specimen starts reproduction and the protocorallite is offsetting for the second time. *a*, calicular view; *b*, side view.

Fig. 4. USNM 196607, ×2. Protocorallite with two generations of offsets. *a*, calicular view; *b*, side view; *c*, view of a very strong attachment and two offsets of a second generation.

Fig. 5. USNM 196608, ×2. Protocorallite producing two generations of offsets. One corallite of the first generation starts reproduction.

Fig. 6. USNM 196571, ×2. Protocorallite with four offsets belonging to two generations (see also text-fig. 1*g*). *a*, calicular view; *b*, side view.

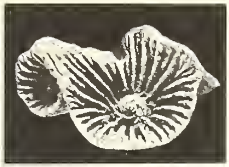
Fig. 7. USNM 196609, ×2. Protocorallite with four asymmetrically arranged offsets of first generation. *a*, calicular view; *b*, side view.

Fig. 8. USNM 196610, ×2. Protocorallite starting to produce offsets very late in ontogeny. *a*, calicular view; *b*, side view.

Fig. 9. USNM 196611, ×2. Corallite with no offsets; only rejuvenescences are produced for a few times. *a*, calicular view; *b*, side view.

Fig. 10. USNM 196579. Protocorallite starting to produce offsets late in ontogeny (see also Pl. 14, fig. 5*a*, *b*). *a*, calicular view, ×2; *b*, side view, ×2; *c*, channels, septal swellings, and new septa on septal pinnacles, ×12.

Fig. 11. USNM 196584, ×8. Bridged channels and a solid partition above them (see also Pl. 14, fig. 10).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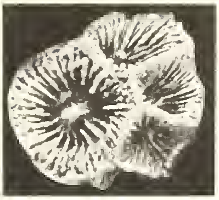
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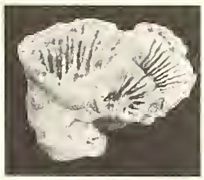
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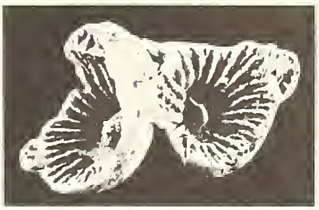
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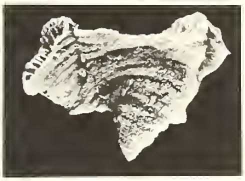
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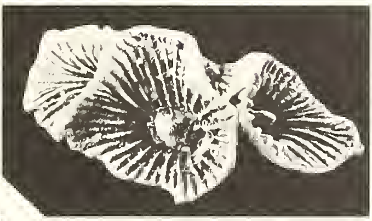
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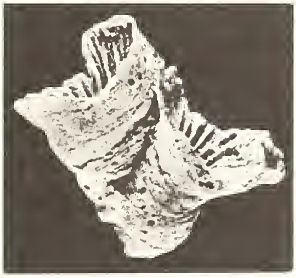
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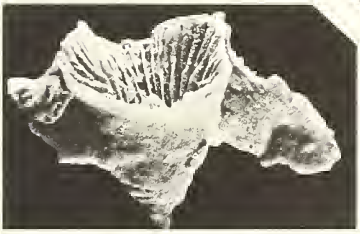
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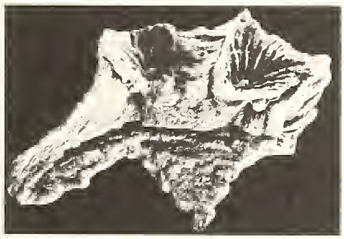
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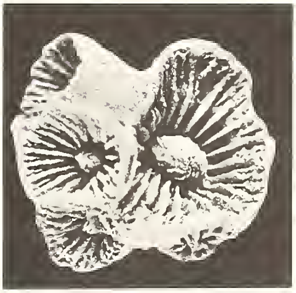
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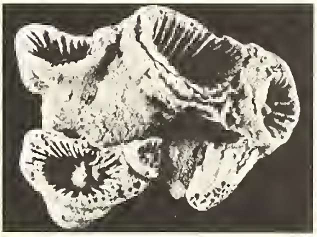
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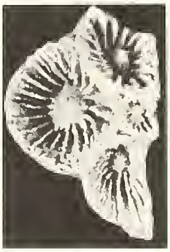
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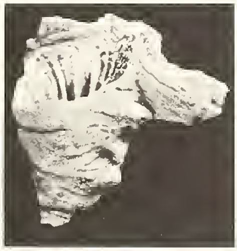
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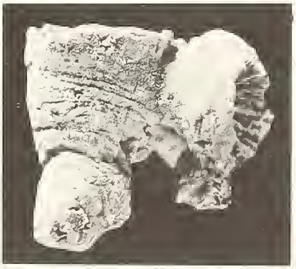
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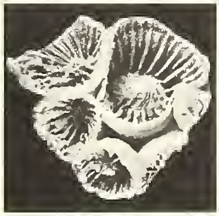
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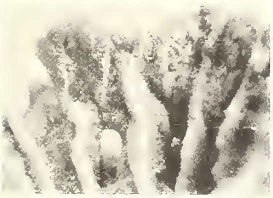
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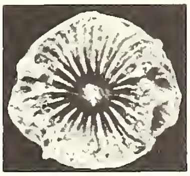
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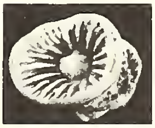
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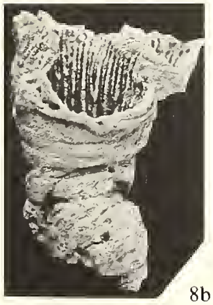
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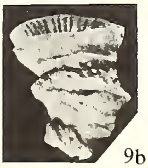
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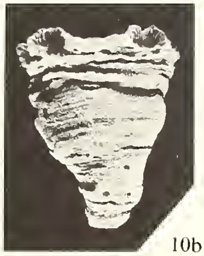
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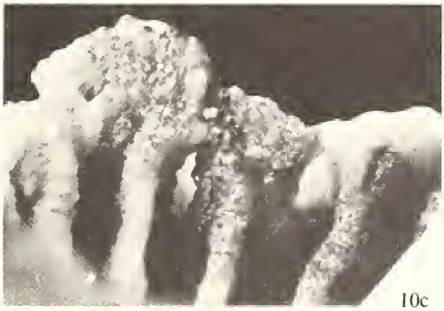
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FEDOROWSKI, coloniality in rugose corals

of astogeny and it is impossible to determine the constancy of this character. It is classified here as an individual variant, mainly because of the morphologic similarities between these and other specimens of the species.

A dividing wall is built along the middle line of a partition by both corallites (Pl. 22, fig. 1). The separation is a slow process, and for a considerable period the young corallite is separated from its parent only by a partition, i.e. calices are separated but the soft tissues remain united above a partition. Heterochronic development of calices has to be noted here, since at the time when the dividing wall was built there were no other structural elements close to it, apart from the upper margin of the partition. All the elements seen in the sections close to the partition and the dividing wall were built later and deeper in the calice.

Division

Division is an abnormal type of asexual reproduction in colonies of the species discussed here. It appears in only a few specimens in the collection under study, and at least three types of origin may be distinguished.

1. In two young protocorallites (Pl. 19, figs. 3, 4) the division may be closely compared with, or is a part of rejuvenescence. In specimen USNM 196625 the polyp lost one-half of its calice and began organizing the second half for two individuals. The wall, based on septa and an axial structure, started to be built in a manner indicating division (Pl. 19, fig. 4). At an early stage, however, the polyp began an unsuccessful rejuvenescence in a very small part of the new calice.

USNM 196624 shows more advanced division which also may be compared with rejuvenescence (Pl. 19, fig. 3). The following characters can be noted: (*a*) approximately one-third of the calice of the protocorallite was lost at the beginning of the division; this is directly comparable with typical rejuvenescence: (*b*) the two newly formed individuals incorporated the rest of the calice of the protocorallite without

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EXPLANATION OF PLATE 17

All figs. × 1·5.

Fig. 1. USNM 196612. Asymmetrical young colony with two offsets of the first generation starting to grow perpendicular to the protocorallite (see also Pl. 23, fig. 11). *a*, bottom view of a strong attachment of protocorallite; *b*, side view of protocorallite and its first offset; *c*, top view showing many shallow rejuvenescences of corallites of a first asexual generation; *d*, calicular view of first and second asexual generations of offsets.

Fig. 2. USNM 196613. Two corallites (probably protocorallites) offsetting only once at early stage of ontogeny.

Fig. 3. USNM 196614. Directed growth of a young colony.

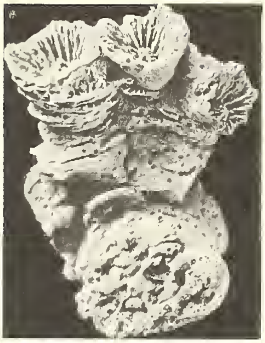
Fig. 4. USNM 196615. Umbrelliform colony with five almost simultaneous offsets. *a*, calicular view of parent corallite; *b*, side view showing an angle of growth of the offsets.

Fig. 5. USNM 196616. Asymmetrical growth of a young colony. *a*, side view; *b*, calicular view.

Fig. 6. USNM 196590. Young colony with crowded corallites (see also Pl. 14, fig. 16).

Fig. 7. USNM 196617. A weak colony with corallites widely spaced.

Fig. 8. USNM 196618. *a*, calicular view of crowded corallites; *b*, view of side opposite to a large, flattened attachment surface.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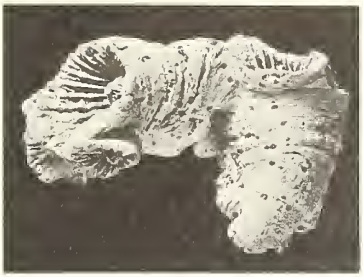
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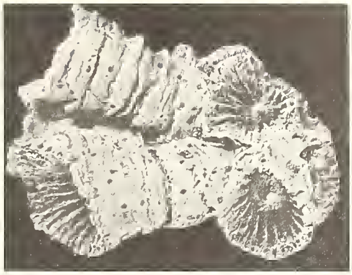
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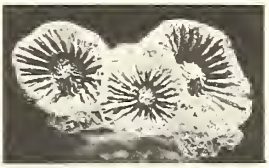
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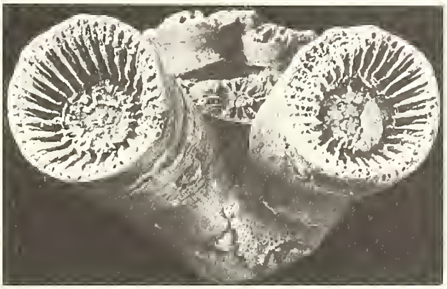
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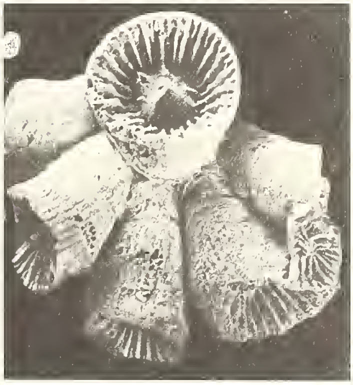
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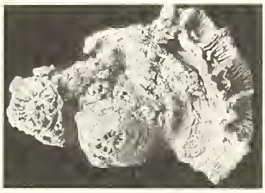
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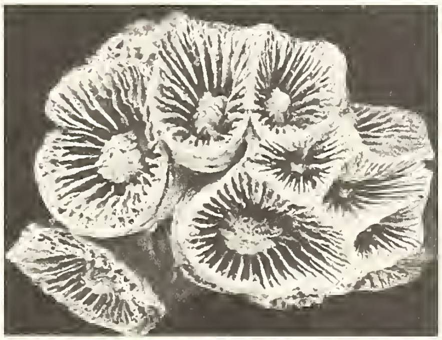
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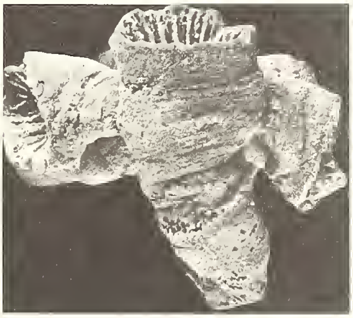
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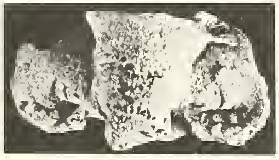
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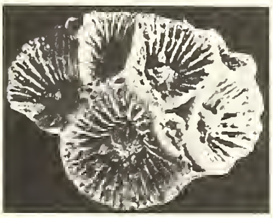
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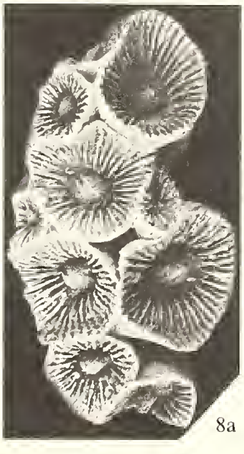
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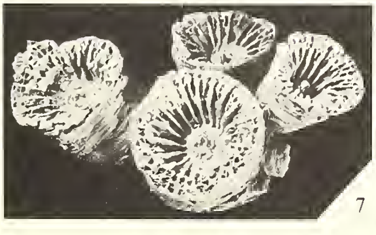
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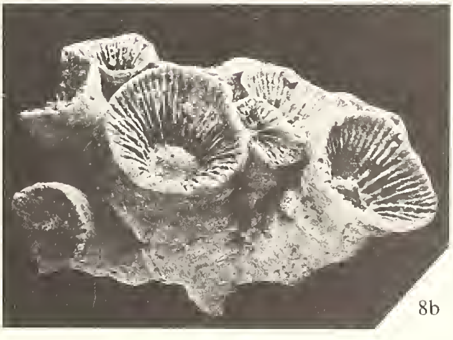

8b

FEDOROWSKI, coloniality in rugose corals

any changes; this is typical of division: (*c*) the new structures formed in the middle of the old calice of the protocorallite have a mixed character. The new wall is similar to the regular wall of a rejuvenescent coral, but it is orientated in the manner characteristic for division. This influences the arrangement of septa inserted on these walls, which are directed towards the two centres.

2. USNM 196622 (Pl. 19, fig. 1) shows an offsetting-like division. The parent corallite is easily recognizable and the offset is produced on a wide, flat shoulder of the parent calice. The arrangement of septa in the common part of both corallites is different from that observed in regularly offsetting specimens. Two long, major septa bend from the margins of the common area towards the axial structure of the parent corallite. Three, most probably new, common parent/offset septa were formed in the space between them. Other septa in the offset side of the common area are established on dissepiments. There was obviously a continuous sheet of soft tissue covering the common skeleton between the two calices.

3. USNM 196623 (Pl. 19, fig. 2*a*, *b*) has a pair of 'twins' produced by the protocorallite of a small colony in which the first series of offsets was regular. At the base of the calice the twins are partly separated by two thickened, straight, major septa. Small, button-like structures on the surface of these two septa are probably new septa of twins. Similar twins have already been described by Jull (1974) in the Australian Lower Carboniferous species *Lithostrotion adjunctum*.

None of the discussed specimens developed by a regular division analogous to that described in Scleractinia, although the development in each example differs from typical offsetting. Division is a rare type of increase in Rugosa and in almost all records I know of it occurs together with other types of offsetting, as an exception. The reason for producing such new individuals is most probably somatic, and may be either pathological or may have resulted from environmental influence (e.g. rejuvenescence-like division). It seems to be insignificant as a taxonomic character. Dr. R. K. Jull (*in litt.*) kindly informs me that he possesses a few incomplete colonies of *L. adjunctum* in which the corallites increase exclusively by division.

Spassky and Kravtsov (1974) applied a new meaning to the term 'division' by including both axial increase and peripheral increase and calling them central division and peripherally calicular division. According to these authors both types of division involve the production of no more than six new individuals since they can be divided only by the protosepta. This seems to be correct as far as the central division (axial increase) is concerned. The septal character of new walls in this type of increase has been discussed many times (e.g. von Koch 1883; Smith and Ryder 1927; Ting 1940;

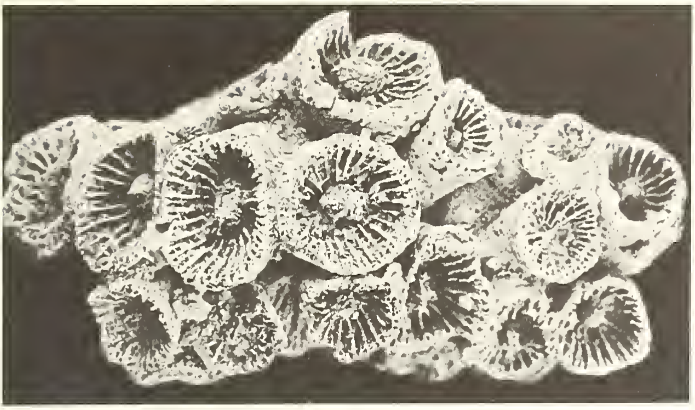
EXPLANATION OF PLATE 18

All figs. × 1·5.

Fig. 1. USNM 196619. Composite colony. *a*, calicular view; *b*, side view.

Fig. 2. USNM 196620. Composite colony. Almost all corallites descend from one protocorallite; the other (lowermost on fig. 2*b*) produced only one lost structure. *a*, calicular view; *b*, side view.

Fig. 3. USNM 196621. Chain-like colony. *a*, calicular view; *b*, bottom view showing two opposite directions of growth of corallites.



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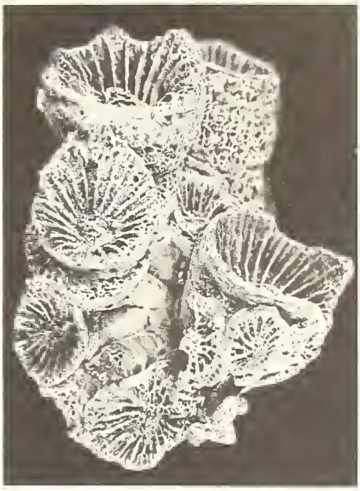

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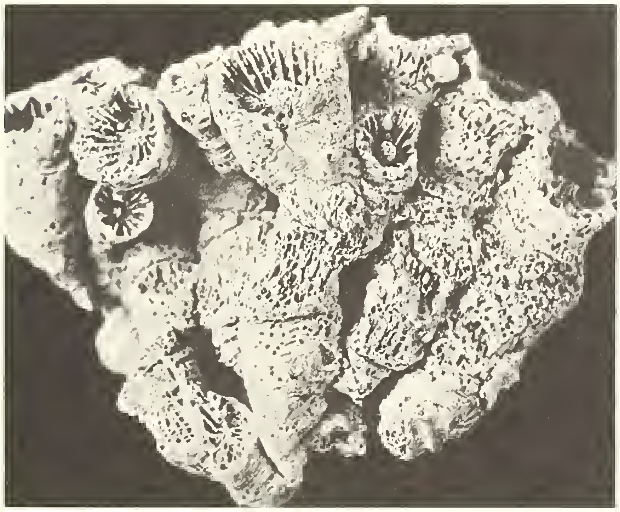

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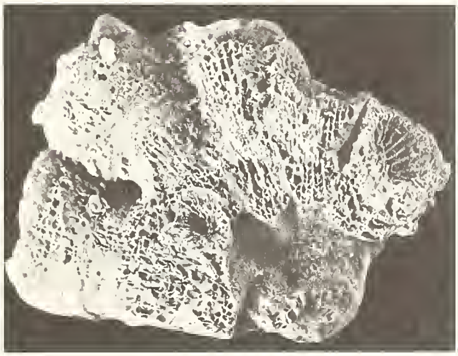

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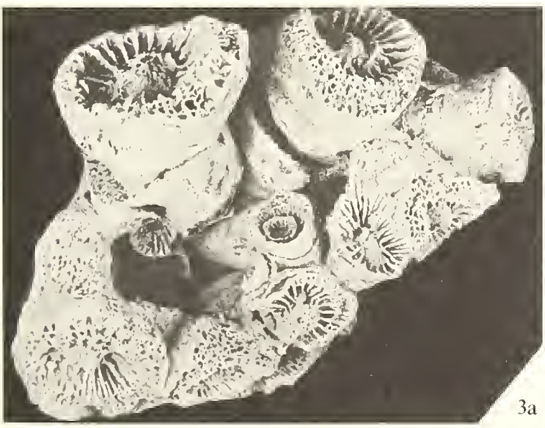

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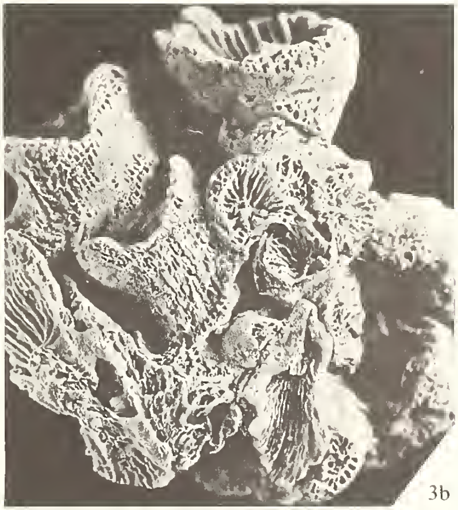

3b

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Hill 1956; Oliver 1968; Fedorowski and Jull 1976). In *Polyadelphia polymera*, Spassky and Kravtsov (1974) showed that there may be either four, or as many as six and as few as two descendent corallites in this type of increase.

However, the other examples given by these authors are not convincing. There is no evidence for a protoseptal (and in general for septal) origin of the new walls. The lack of detailed study on any of the examples shown by Spassky and Kravtsov (1974) makes it impossible to reliably establish the origin and development of the types of increase mentioned by them. It seems probable, however, that the examples shown by them on their plate 2, figs. 2, 3 and possibly also fig. 4 represent division of a twin-type, while those on their plates 3 and 4 represent peripheral increase. Some examples of peripheral increase studied in detail by Jull (1965) and Fedorowski (1970) show that there may be more than six descendent corallites formed, and that they are clearly not connected with the protosepta as suggested by Spassky and Kravtsov (1974).

The terms axial increase and peripheral increase could be called 'division' as used by Spassky and Kravtsov in that the old polyp is divided into new ones. However, at first the origin of a central division (axial increase) differs from peripherally calicular division (peripheral increase; e.g. compare the schematic reconstructions of Fedorowski and Jull 1976), and there is no need to use new names for these reasonably well-known processes. This is especially so in this case when the proposed name 'division', is actually used for a rare, very variable, and taxonomically unimportant process in Rugosa, and also for an important process of different origin in Scleractinia.

Lost structures

This is a new term proposed here for any offset produced in the process of lateral increase and left underdeveloped far below an actual margin of the parent calice, with no evident external factors acting to stop its development. This definition expresses three main characters of these structures: (*a*) the progeny is never parricidal; (*b*) the progeny may reach varying stages of hystero-ontogeny ranging from the hystero-brephic to hystero-neanic stages. It dies underdeveloped, although the

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EXPLANATION OF PLATE 19

Fig. 1. USNM 196622, × 3. Offsetting-like division on shoulder of calice.

Fig. 2. USNM 196623. Colony with regular offsets and 'twins'. *a*, calicular view, × 1·5; *b*, calicular view of the 'twin' type of division showing two major septa converted into walls which partly separate the 'twins', × 3.

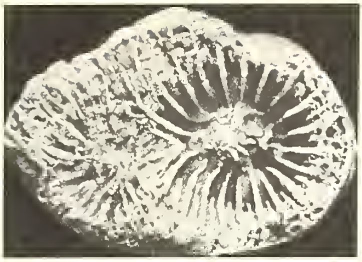
Fig. 3. USNM 196624, × 4·5. Combination of rejuvenescence and division. New walls have no relation to parent septa and are supported by a skeleton of the old axial structure.

Fig. 4. USNM 196625, × 4·5. Initial stage of division and rejuvenescence taking place in axial part of an old calice.

Fig. 5. USNM 196626. Probable protocorallite (proximal end not preserved) with a lost structure produced by division. *a*, side view, × 1·5; *b*, calicular view of the lost structure showing its own rejuvenescence and a close relation to a shallow rejuvenescence of a parent corallite, × 3.

Fig. 6. USNM 196572, × 1·5. Protocorallite offsetting only once during its ontogeny (see also text-fig. 1*h*).

Fig. 7. USNM 196627, × 1·5. A quasi-colony. *a*, protocorallite with two generations of offsets; *b*, fragment of protocorallite with an offset produced by division.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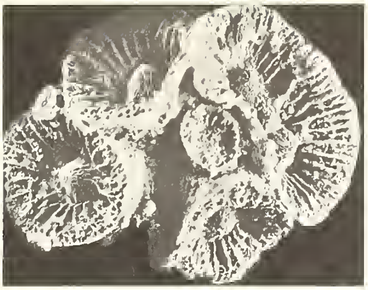
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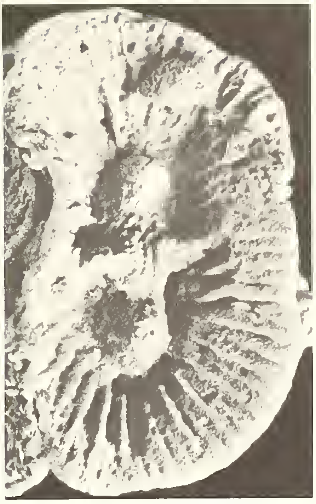
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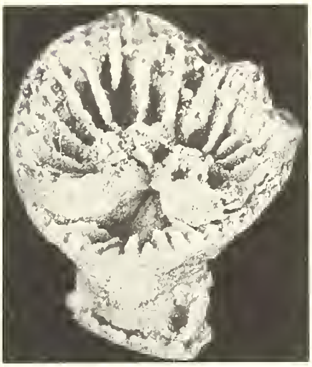
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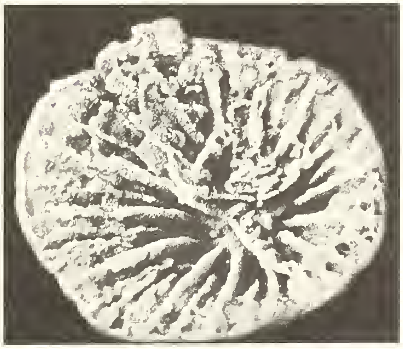
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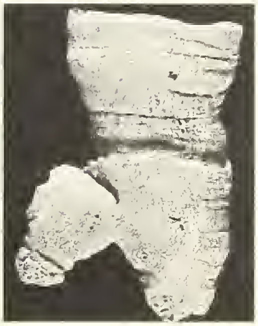
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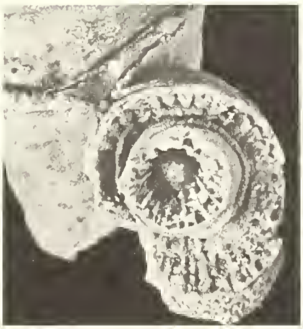
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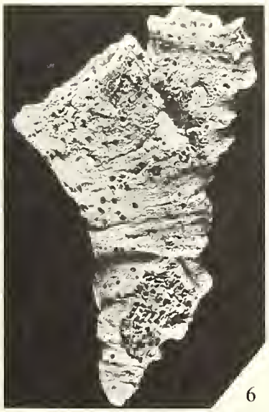
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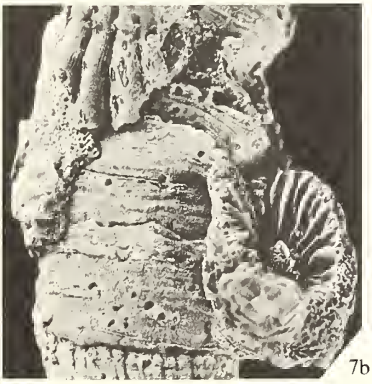
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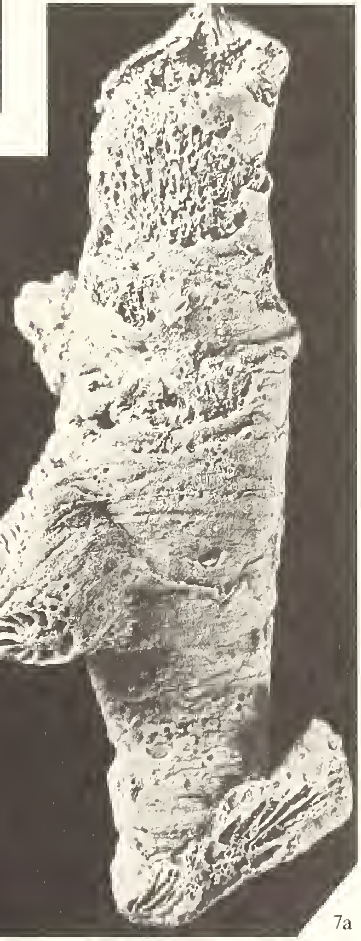
7a

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parent continues to grow under the same external conditions; and (*c*) there is no fundamental difference between the lost structure and any normal, lateral offset in their increase, insertion of septa, and appearance of other structural elements, except that they did not reach morphological maturity. The reason for this underdevelopment is assumed to be genetic.

The above statements exclude all corals that produce peripheral offsets. Peripheral increase is parricidal, and the offsets, although underdeveloped in many known examples (e.g. Jull 1965; Fedorowski 1967*b*, 1970; Minato and Rowett 1968), cannot be compared with lost structures. In fact, being a multiple continuation of a parent corallite, offsets in peripheral increase are opposite to lost structures.

There are also laterally produced offsets which are not lost structures although they also died underdeveloped. Their underdevelopment is due to external factors, such as the rotation or fall of a colony to put the young corallite into sediment. Although similar to lost structures, these should be distinguished since they obviously have no genetic significance. The material described here includes many examples of both lost structures (Pl. 19, figs. 5*a*, *b*, 7*a*, *b*; Pl. 23, figs. 7, 9*a*, *b*, 11, 12) and young corallites that died early because of extrinsic factors (Pl. 15, figs. 8–14; Pl. 16, figs. 1–7; Pl. 18).

Offsets comparable with lost structures have rarely been reported in the literature. Offsetting in '*Caterophyllum*' *verticillatum* Barbour, 1911, studied in detail by Fagerstrom and Eisele (1966), and in *Timania rainbowensis* Rowett, 1969, studied from the aspect of asexual reproduction by Minato and Rowett (1968), seem to be the only known examples. Minato and Rowett grouped together some laterally and peripherally increased corallites and called them 'simple budding' forms. They equated this term with 'quasi-colonies' of Fagerstrom and Eisele. I take the view that '*Clisaxophyllum*' *awa atetsuense* and most probably also *Lonsdaleoides*(?) *nishikawai*, as described by Minato and Rowett, represent peripheral increase and as such should be called incipient colonies (term introduced by Fedorowski 1970), whereas 'colonies' of *T. rainbowensis*, which show significant similarity to '*Caterophyllum*' *verticillatum*, belong to 'quasi-colonies'. The term 'simple budding' seems to be too general since it includes quite different modes of offsetting, and it is not adopted here.

EXPLANATION OF PLATE 20

Fig. 1. USNM 196628, × 1·5. Axial rejuvenescence in quasi-colony (see also Pl. 23, fig. 12).

Fig. 2. USNM 196629, × 1·5. Directed growth of part of a colony. *a*, calicular view showing an axial (*right*) and lateral (*centre*) rejuvenescence, and a combination of lateral rejuvenescence with offsetting (*left*); *b*, side view of parent and offset corallites; *c*, bottom view of umbrelliform arrangement of offsets.

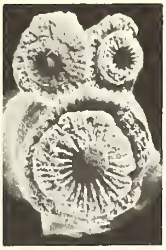
Fig. 3. USNM 196630, × 1·5. Axial rejuvenescence and a directed growth of offsets.

Fig. 4. USNM 196631. Very deep narrowings of growth. *a*, side view, × 1·5; *b*, continuation of external wall on the flat, horizontal surface of narrowed skeleton, × 3.

Fig. 5. USNM 196632, × 1·5. Attachments of particular corallites inside a fasciculate colony.

Fig. 6. USNM 196633, × 1·5. Calicular view of colony showing axial and lateral rejuvenescences. The lower right calice shows three new individuals, which appeared in a way comparable with both rejuvenescence and peripheral increase.

Fig. 7. USNM 196634, × 1·5. A weak, simple colony showing directed growth. The protocorallite (*right*) is the only large corallite, but one of the offsets of the first asexual generation also attained the capacity to reproduce.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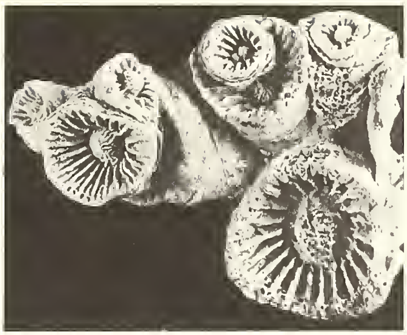
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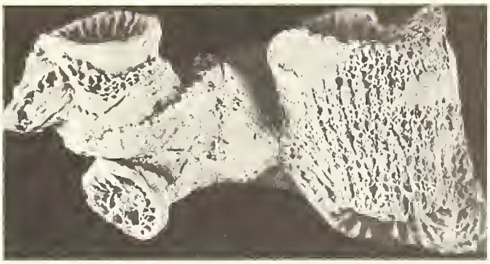
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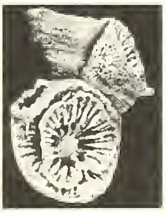
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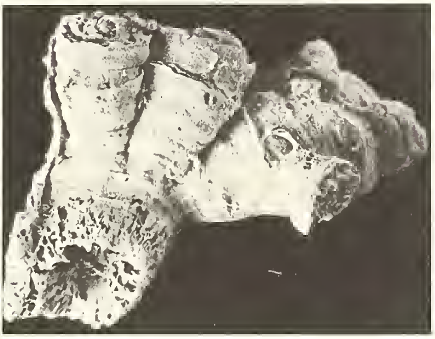
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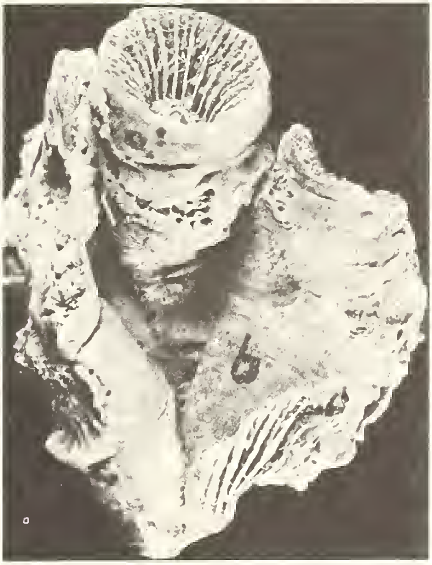
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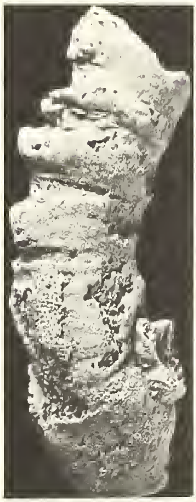
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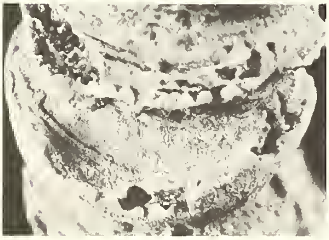
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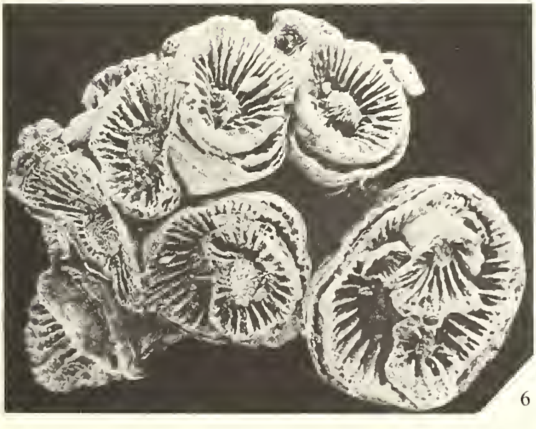
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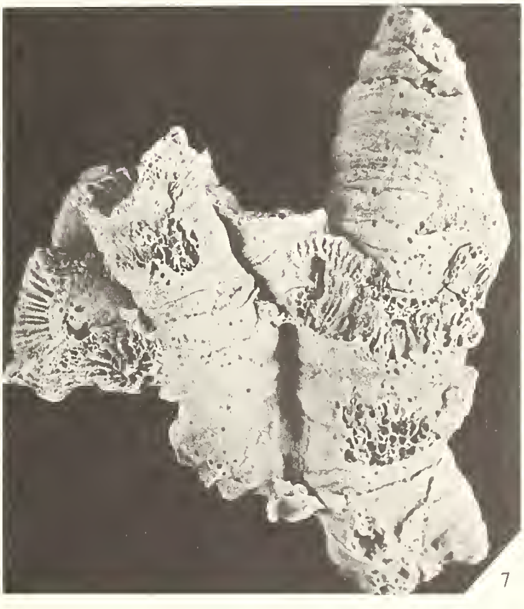
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Lost structures appear most commonly, but not exclusively, in connection with rejuvenescence. Similar observations were made by Fagerstrom and Eisele (1966, p. 595), who wrote: 'Rejuvenescence of protocorallites commonly occurs directly above each verticil. In addition to buds in verticils, many protocorallites bear buds randomly arranged between verticils or with random arrangements of buds throughout.' In some cases the polyp of a lost structure may be rejuvenated (Pl. 19, fig. 5*b*; Pl. 23, fig. 9*b*) or even produce its own offset (Pl. 19, fig. 7*a*). Nevertheless, it did not reach morphological maturity and died shortly after losing its direct soft-tissue connection with the body of the parent polyp. This direct dependence of a polyp of lost structure on that of a parent may be regarded as one of the main reasons for their early extinction. This is especially obvious in the case of rejuvenescence of a parent (Pl. 19, fig. 5*a*, *b*).

Observations of lost structures indicate that they are neither produced incidentally (since they show all characters of offsets), nor regular, healthy offsets, capable of reaching morphologic maturity. It seems likely that there are some species of solitary corals, or some populations, that possess the genetic potential to produce offsets. This is not a first-range character, however, and in regular circumstances it is suppressed by other characters. *T. rainbowensis* may be cited as an example. The genetic potential to produce offsets seems to be only initially developed in this species and its usage is probably stimulated by extrinsic factors. '*C.*' *verticillatum*, although generally a solitary species, represents a more advanced stage of development of genetic potential to produce offsets. There are a number of corallites within this species offsetting many times during their ontogeny. However, none of them form a normal, healthy colony.

As far as I know no offsets comparable with lost structures have yet been reported from well-developed colonies. In the collection of *Heritschioides* sp. nov. discussed here, there is no well-developed colony in which any underdeveloped offset can definitely be called a lost structure. These structures are especially common in quasi-colonies (Pl. 19, figs. 5*a*, *b*, 7*a*, *b*; Pl. 21, figs. 8, 9; Pl. 23, figs. 9*a*, *b*, 12) and much less frequent in simple colonies, i.e. normal colonies resulting from a lateral increase, but developing very few branches during astogeny (Pl. 20, fig. 7; Pl. 23, fig. 11).

EXPLANATION OF PLATE 21

All figs. × 1·5.

Fig. 1. USNM 196635. Circumrotary colony. *a*–*c*, different sides showing differentiated directions of growth of corallites.

Fig. 2. USNM 196636. Very late offsetting of a protocorallite showing a combination of deep axial rejuvenescence and lateral offsetting. *a*, calicular view; *b*, side view.

Fig. 3. USNM 196637. Non-offsetting protocorallite attached to inner surface of brachiopod shell.

Fig. 4. USNM 196638. Small hemispherical colony with crowded corallites.

Fig. 5. USNM 196639. Pseudo-colony with offsetting 'guest' corallite.

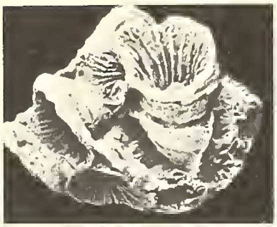
Fig. 6. USNM 196640. Protocorallite offsetting for first time at late ephebic stage.

Fig. 7. USNM 196641. Composite colony. A few corallites attached to the calice of a dead individual.

Figs. 8, 9. USNM 196642–196643. Quasi-colonies.

Fig. 10. USNM 196644. Probably a composite colony. Progeny of two protocorallites tend to grow together.

Fig. 11. USNM 196645. Chain-like colony.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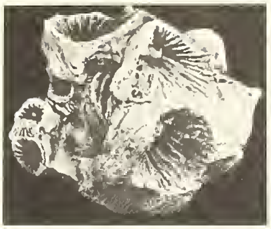
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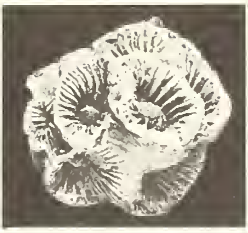
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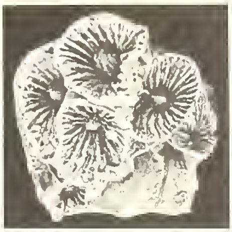
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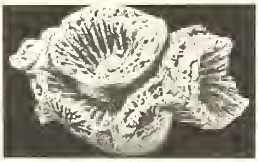
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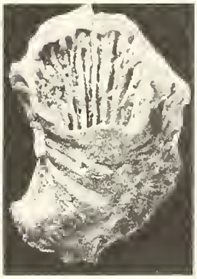
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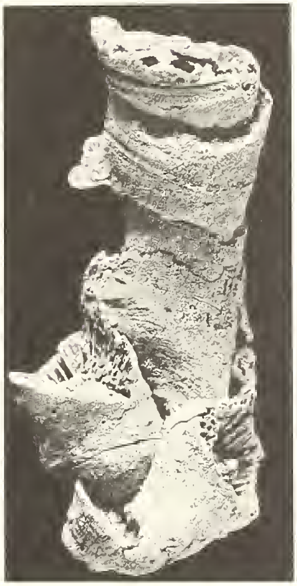
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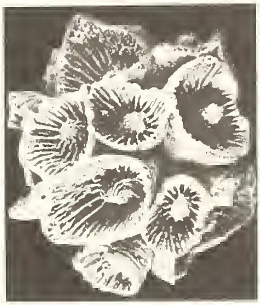
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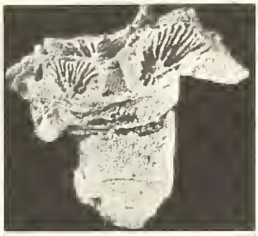
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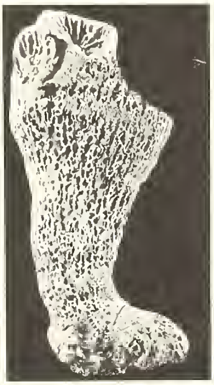
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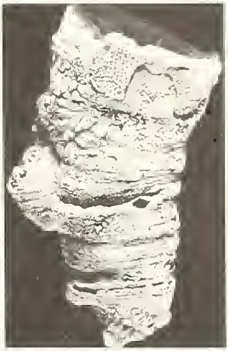
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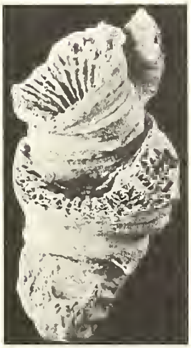
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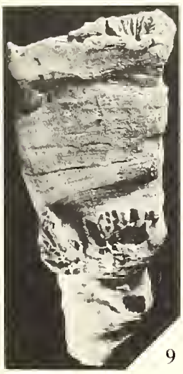
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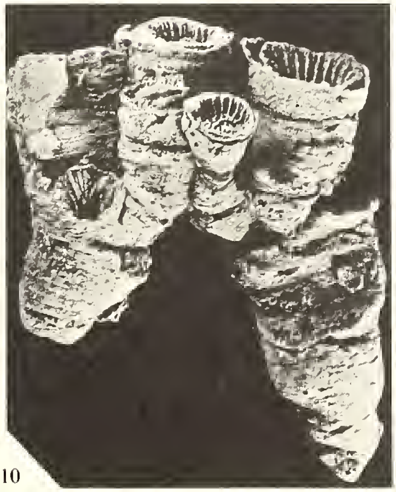
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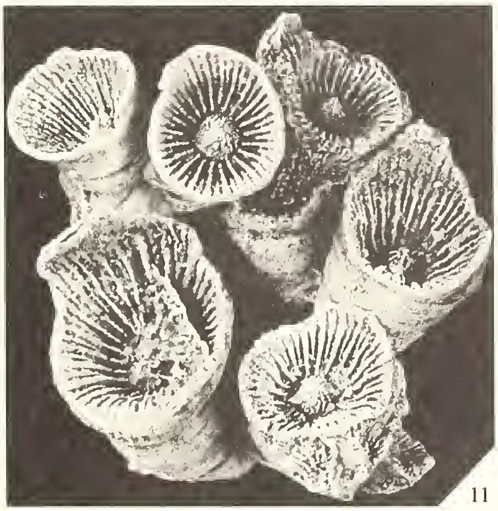
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FEDOROWSKI, coloniality in rugose corals

Heritschioides sp. nov. belongs to the type of colonial species in which a group of individuals may possess only a weak ability to produce offsets. This capability may be developed to a different degree in different specimens and in some of them it is also suppressed by other characters, as discussed above for the solitary corals. Similar results may thus be achieved in the development of a colony, although from opposite origins. In the one case a 'colony' (mainly quasi-colony or incipient colony) originates from a solitary coral, while in the other it originates from a protocorallite of a generally colonial species, in which the character of coloniality, weakly fixed in its genetic code, is suddenly stimulated. Such a protocorallite or solitary corallite polyp, although capable of creating a daughter polyp, is not able to provide it with the complete genetic potential for regular development. As a result the daughter polyp cannot mature.

In all three species discussed above (*Heritschioides* sp. nov., '*C.*' *verticillatum*, and *T. rainbowensis*), solitary corallites with no offsets produced at any stage of ontogeny are also known to occur. The frequency of such corallites is greatest in *T. rainbowensis*, which is primarily solitary and belonging to a solitary genus, and least in *Heritschioides* sp. nov., which is generally colonial, and belongs to a colonial genus. This indicates that the types of structures discussed and an initial coloniality may appear either as an incipient character or as rudimentary feature. In both cases it is marked by similar types of offsets—i.e. lost structures.

REJUVENESCENCE

This is a common process permitting a prolongation of existence of particular corallites within colonies. As there is only a quantitative difference, any example in which a polyp loses a part of its old calice and starts to build a narrower one without either dividing its soft body or opening a new mouth, should be called rejuvenescence. It may happen only once, or it may take place with irregular frequency during the hystero-ontogeny of particular corallites. It may be weak or intensive, i.e. smaller or greater parts of the old calices may be lost and replaced by new structures.

There are many examples of '*shallow*' and *irregular rejuvenescence* within the collection, such as some parts of the corallites shown on Plate 14, fig. 17; Plate 17, fig. 1; Plate 20, figs. 1, 7; Plate 21, fig. 8; and Plate 22, fig. 8. Such rejuvenescence may involve the whole circumference of the calice, or only a part of it. The external wall, outer parts of the dissepimentarium, and peripheral parts of septa, are the morphological structures which are lost during the process. The new wall bounds remaining parts of the calice. The whole rejuvenescence of this initial type resembles a regular but deep growth line of the external wall. The only difference is that in rejuvenescence the external wall loses its continuity. This may happen when the polyp is diminished rapidly, but not deeply, instead of contracting gradually. In some cases the margin of the old calice is slightly deflected inwards (Pl. 23, figs. 1*a*, *b*), indicating that the regular process of reduction in size had started and was replaced by rejuvenescence. All more axially located skeletal elements remain unchanged in any of the above examples. There are also quite remarkable decreases in observed diameter that did not cause a break of the external wall, but the wall continued to grow almost horizontally into the calice (Pl. 20, fig. 4*a*, *b*).

The next stages of change in skeletal morphology during rejuvenescence are seen in the collection but only the final steps are described here since the intermediate stages can easily be deduced. Two types of rejuvenescence are observed in which a large part of the calice is involved. They may be given names parallel to those referring to types of offsetting, i.e. *axial rejuvenescence* and *lateral rejuvenescence*. These types are not as constant as in blastogeny and intermediate examples are known.

In *axial rejuvenescence* the central part of the corallite, the axial structure, and the axial parts of the major septa, and most probably also the central part of the polyp, remain in place and are almost unchanged. The number of lamellae in the axial structure may be reduced, or the thickness of septa may be changed, but these changes are not fundamental. The whole external ring of the calice, i.e. the dissepimentarium, the minor septa, and the external parts of major septa were lost. The diminuted polyp started its new stage of development with a mixed skeletal morphology—an advanced internal part and a juvenile, often thickened, peripheral part. This type of rejuvenescence may take place many times during the development of particular corallites (Pl. 19, fig. 5*b*; Pl. 20, figs. 1, 3, 6; Pl. 22, figs. 10*a*–*c*, 12).

Lateral rejuvenescence (Pl. 20, figs. 2*a*, 6; Pl. 21, fig. 7; Pl. 22, fig. 7) takes place where a given part of the periphery of the old calice remains unchanged. This is common in the collection under study. The polyp retained approximately one-half of its skeleton and built a new external wall within the old calice. The axial structure, which is not included in the new calice, seems to be a mechanical support for the new external wall (Pl. 22, fig. 4). Also in this type of rejuvenescence the new corallite possesses a mixed skeleton. The polyp retained a part of the old external region of the calice and built a new axial structure and new structural elements on the inner part of the calice.

All these types of rejuvenescence seem to be similar in one important feature, viz. a new mouth is not opened and the oral disc, as well as the remainder of the soft tissue, is not divided since the number of septa present before, during, and after rejuvenescence remains more or less the same.

There are a few significant irregularities in rejuvenescence within the collection. In some specimens (Pl. 22, fig. 3) it is impossible to determine how much of the calice was lost as there is no wall separating the presumed surviving part from the rest of the calice. On the other hand, there is only a very limited part of the corallite which obviously continued to grow, and in this part a new axial structure was built.

An initial stage of simultaneous offsetting and rejuvenescence is shown in Plate 22, fig. 8 and a more advanced one in Plate 21, fig. 2*a*, *b*, and Plate 22, fig. 7. In the last example, the offsets are lost structures that ceased to develop as soon as the polyp lost the near-by part of the calice which was starting its rejuvenescence.

There is also another example of renovation, closely resembling rejuvenescence, but which should not be equated with it. This occurs when more than one individual develops from the old one, indicating that new mouths had been opened. This is very similar to peripheral increase in regular offsetting, and in fact should be compared closely with that process. However, it is sometimes obviously connected with rejuvenescence, as shown in Plate 20, fig. 6 (lower-right corner). This may be additional support for the Fedorowski and Jull (1976) thesis that peripheral increase should be treated in most cases as multiple rejuvenescence. The process in this case is so deep that it leads to the fragmentation of the soft tissue and to the loss of part of it.

ASTOGENY

Offsetting and the problem of maturity

Maturity in previously described types of colonies. The problem of determining maturity in Rugosa is very important since only comparison of mature corallites can establish intraspecific variability, boundaries of species or subspecies, etc. At the same time the problem is difficult to solve since there are no common criteria to use for all groups of corals. The problem of maturity is especially important in colonial species, in which variability within the colony is superimposed on intraspecific variability.

It is generally accepted that the capacity to produce offsets is one of the best criteria of maturity. In most colonies previously studied in detail (e.g. Smith 1915; Smith and Ryder 1926, 1927; Różkowska 1960; Jull 1965, 1967, 1974*a*, *b*; Fedorowski 1965, 1967*a*) one can observe many examples. Offsetting corallites within the colony may differ a little from each other in their morphology and measurements, but almost all are presumed to be secreted by mature polyps. Probably the only youthful offsetting individual yet reported is that illustrated by Jull (1974*a*, fig. 7_2). There are also other corallites in normally developed colonies, the polyps of which did not reproduce asexually although their structure and measurements are similar to those of offsetting specimens (Fedorowski 1965; Ulitina 1974). In some colonies there is only one, or just a few corallites producing offsets (Beklemishev 1958). This phenomenon is not yet adequately investigated and requires more careful study, especially the comparison between otherwise similar offsetting and non-offsetting

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EXPLANATION OF PLATE 22

Fig. 1. USNM 196646, ×3. Partition separating two corallites is replaced by a dividing wall.

Fig. 2. USNM 196647, ×1·5. Rapid narrowing of a calice.

Fig. 3. USNM 196648, ×1·5. Lateral rejuvenescence in very limited area of an old calice.

Fig. 4. USNM 196649, ×3. Deep rejuvenescence. Bottom of a new calice hangs on an old axial structure.

Fig. 5. USNM 196650, ×9. Partly overgrown channel (indicated by arrow) with 'interrupted' minor septum.

Fig. 6. USNM 196651. *a*, probable quasi-colony, ×1·5; *b*, offsets separated from parent by dividing walls. The left offset is united with the parent by bottom channels, ×3; *c*, part of calice showing open (1, 2) and partly overgrown (3, 4) channels, ×7·5.

Fig. 7. USNM 196652, ×3. Contemporaneous deep, lateral rejuvenescence and offsetting.

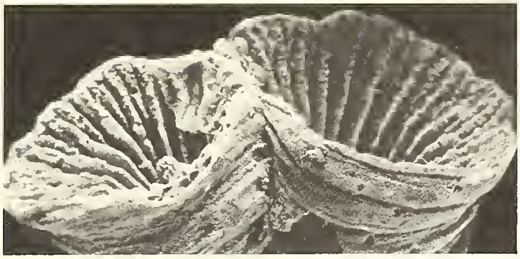
Fig. 8. USNM 196653, ×1·5. Contemporaneous shallow rejuvenescence and offsetting.

Fig. 9. USNM 196654, ×3. Marginal rejuvenescence on wide shoulder of calice.

Fig. 10. USNM 196655. Cyclic rejuvenescence. *a*, calicular view, ×1·5; *b*, side view, ×1·5; *c*, axial view showing relation between external and internal parts of major septa and new wall, ×4·5.

Fig. 11. USNM 196656, ×7·5. Relationship between septa in old and rejuvenated calices, and position of a new wall, convex outwards.

Fig. 12. USNM 196657, ×1·5. Composite colony showing axial rejuvenescence of corallites.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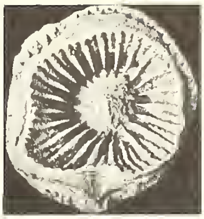
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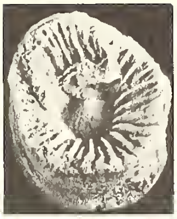
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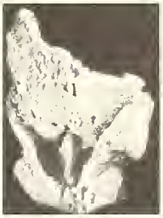
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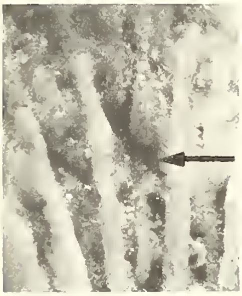
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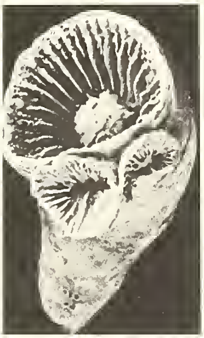
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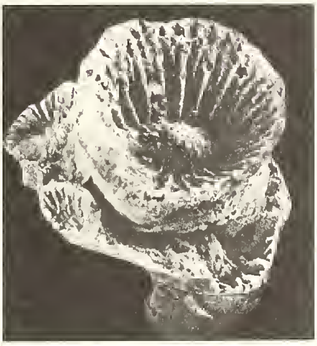
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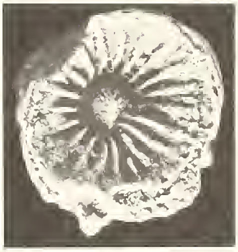
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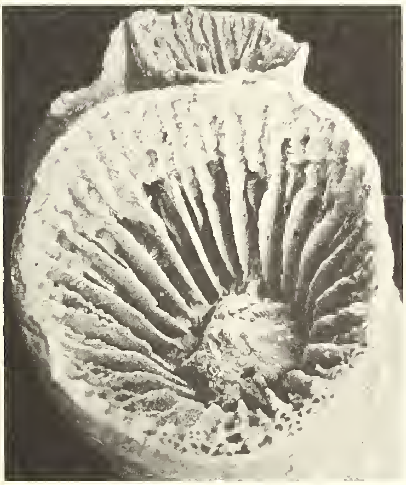
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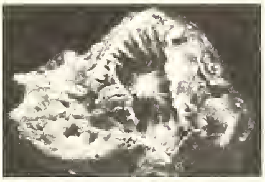
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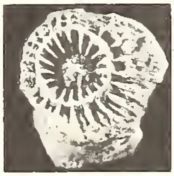
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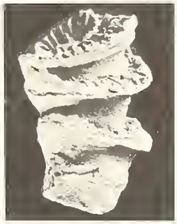
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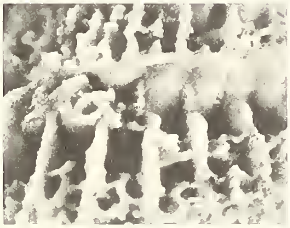
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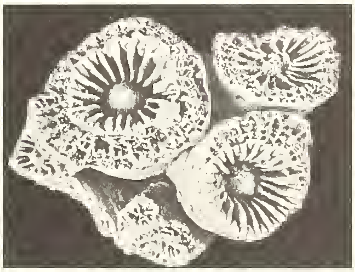
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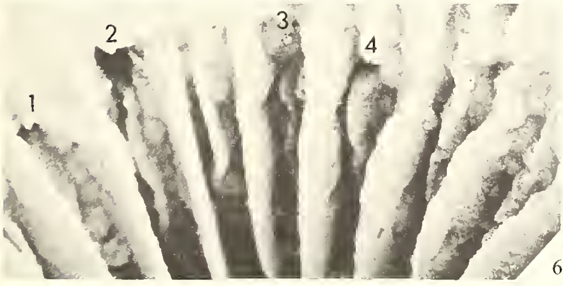

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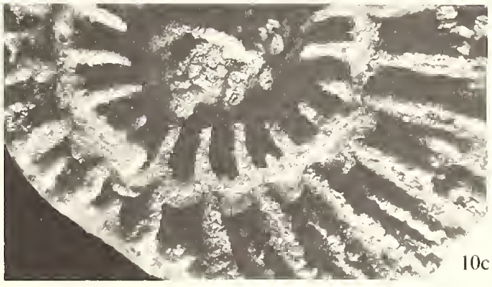
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FEDOROWSKI, coloniality in rugose corals

corallites. Both types of corallites seem to be morphologically mature, but as yet the factors that stop offsetting in one group are unknown.

In addition to normally developed colonies there are at least two types of 'coloniality' known, which can only be classified formally as colonies. They are the quasi-colonies and incipient colonies discussed above. Colonies of '*Craterophyllum*' *verticillatum* Barbour, studied in detail by Fagerstrom and Eisele (1966), provide almost all the known information on quasi-colonies. In these colonies the protocorallite is the only morphologically (and most probably also sexually) mature individual, and the offsets never reach the degree of development of the protocorallite, although they may be quite numerous and may be produced many times during the development of the protocorallite. These offsets are the lost structures described earlier.

Incipient colonies studied by Jull (1965) and Fedorowski (1967*b*, 1970) appear in some solitary corals (e.g. *Ceratophyllum*, *Spirophyllum*) and show another aspect of the problem of maturity in Rugosa. There is no second generation of offsets produced in such 'colonies', and the corallites of the asexually produced generation are, almost without exception, morphologically underdeveloped compared with the protocorallites. In this sense incipient colonies may be compared with quasi-colonies, as the protocorallites are the only completely developed individuals in both of them. This is the only similarity, however, since modes of offsetting and the reason for extinction of progenies are entirely different.

Maturity of solitary corallites and protocorallites in Heritschioides *sp. nov.* The collection contains hundreds of specimens in different stages and types of astogeny, as well as solitary corals. All of these specimens are here considered to belong to one species and one population. Some of the solitary corals are immature since they possess either obviously juvenile characters, or their mature characters are underdeveloped. Some of them are not immature since they are morphologically advanced in ontogeny and have structures and dimensions (text-fig. 5B) typical for colonial corallites that are most advanced in hystero-ontogeny. Since this species is generally colonial, solitary corals in the population should be regarded as potential protocorallites with protopolyps in which the capacity to produce offsets has not been realized.

In most of the well-preserved young colonies, a first offset appears on the protocorallite after 4–6 mm of growth, but it may appear as early as after approximately 2 mm (USNM 196692). The protocorallite is very juvenile in character when its protopolyp offsets so early. It does not possess a dissepimentarium, and the arrangement of its septa is zaphrentoidal with the axial structure at an early stage of development (Pl. 15, figs. 9*a*, 10*a*). The protopolyp is the only individual within the colony having the capacity to produce offsets at such a young stage of ontogeny. In Tables 1–3 the basic measurements of representative specimens are given to show similarities and differences among offsetting specimens in particular stages of astogeny.

Protopolyps that begin to produce offsets during the middle or late neanic stage of morphological development possess protocorallites with a dissepimentarium built of one or a few verticils of dissepiments, a quite well-developed axial structure, and radially arranged septa (Pl. 15, figs. 12*b*, 13*b*, 14). Protocorallites, the protopolyps of which started to produce offsets while in an advanced stage of ontogeny, are rare in the material studied (Pl. 16, figs. 8*a*, *b*, 10*a*, *b*; Pl. 19, fig. 6; Pl. 21, fig. 6). In some cases

TABLE 1. *a*, Solitary corallites.

Specimen number	Length	Diameter of calice	Number of septa	Remarks
196671	6·1	4·6 × 4·0	12 – 14?	
196670	8·1	6·2 × 5·3	18 × 2	
196673	12·1	10·1 × 8·4	19 × 2	
196666	23·2	8·8 × 8·5	21 × 2	
196674	26·1	9·9	22 × 2	Calice broken in p–t
196660	12·1	11·0 × 8·3	22 × 2	
196637	19·0	11·4 × 10·0	22 × 2	
196672	33·0	11·8	24 × 2	Calice broken in p–t

b, Protocorallites with hystero-brephic stages of first offsets.

Specimen number	Length	Diameter of calice	Number of septa	Remarks
196600	3·7	5·2 × 4·1	15 – 16 × 2	
196568	4·3	5·2 × 4·4	16 × 2	
196675	5·6	5·1 × 3·4	15 × 2	
196602	7·2	6·9 × 5·5	17 × 2	
196580	7·4	6·9 × 5·5	17 × 2	
196595	7·5	7·0 × 5·7	15 – 16 × 2	
196596	8·8	7·4 × 6·2	19 × 2	
196579	13·5	11·8 × 10·6	21 × 2	

c, Colonies in which first asexual generations of corallites start to produce offsets.

Specimen number	Length	Genera-tion	Diameter of		Number of septa	Remarks
			Firstly offset. pc	Calice		
196606	13·2	pc	3·7 × 3·4	8·0 × 8·0	22 × 2	
	11·4	a		10·8 × 6·7	20 × 2	
196668	11·3	pc	4·8 × 4·0	12·8 × 9·2	22 – 23 × 2	
	10·5	a		11·4 × 8·2	20 × 2	
	7·5	b		10·5 × 6·5	19 × 2	
	6·0	c		9·1 × 6·7	19 × 2	Not offsetting
196618	21·0	pc	4·0 × 3·0	12·3 × 10·7	24 × 2	
	18·2	a		12·0 × 9·5	22 × 2	
	15·5	b		10·0 × 9·4	22 × 2	
	15·0	c		8·9 × 8·7	21 × 2	Not offsetting
	?	d		7·2 × 6·6	19 × 2	Not offsetting
	10·7	e		8·0	?18	Not offsetting
196608	8·5	pc	5·8 × 6·0	8·5 × 4·5	20 × 2	
	8·8	a		7·3 × 4·5	18 × 2	Not offsetting
	10·5	b		9·5 × 9·0	21 × 2	
196616	11·5	pc	6·5 × 6·0	11·8 × 10·5	26 × 2	
	8·0	a		10·3 × 8·8	20 × 2	
	6·0	b		8·3 × 7·1	19 × 2	
	6·0	c		8·0 × 5·0	16 × 2	Not offsetting
	9·0	d		9·8 × 7·6	20 × 2	

See Table 4 for explanation of abbreviations.

they produced many offsets almost simultaneously around the shoulder of the calice (Pl. 16, fig. 10*a*, *b*), but they may have produced only one offset (Pl. 19, fig. 6).

Judging from these observations, there is no simple relationship between capacity to produce offsets and the stage of morphological development of the protopolyp and its protocorallite. Protopolyps of all the protocorallites discussed attained the capacity to produce offsets at quite different stages. This being so, is it reasonable to regard this character as diagnostic of maturity?

No general answer is currently available. It is possible to assume, however, that such a wide variability of so important a character as asexual reproduction must have been fixed in the genetic code of polyps, and that not only was an opportunity to produce offsets coded, but also its potential or degree of necessity. These factors, together with environmental influences which suppressed or emphasized them, resulted in the situation discussed above. Therefore it seems necessary to distinguish two kinds of maturity of protocorallites: 1, morphological maturity, i.e. the stage at which the protocorallite reaches the highest degree of individual development, but does not start to degenerate gerontically; and 2, the capacity to produce offsets. This may be reached at different stages of ontogeny and is individual. This character may not develop at all when not strongly fixed in the genetic code, and the polyp then produces only a solitary corallite. In this case the potential to produce offsets may be suppressed by an environmental influence.

Maturity of asexually produced corallites in Heritschioides *sp. nov.* As noted earlier, most of the protopolyps were in an early stage of ontogeny when they first produced offsets. Supposing this to be a rule, one can observe that the first asexually produced generation reached its capacity to produce offsets at a more advanced stage of morphological development than the protopolyps. Corallites of this generation possess a dissepimentarium and well-developed axial structure. They do not show any clearly juvenile characters but their polyps almost always begin their asexual reproduction before reaching complete morphological maturity (Pl. 16, figs. 3, 5).

TABLE 2. Separate, subcylindrical corallites.*

Specimen number	Actual length	Diameter of calice	Number of septa	Remarks
196681	33·5	19·0 × 16·6	25 × 2	
196682	33·0	19·5 × 17·7	23 × 2	
196683	52 × 5	15·8 × 15·0	24 × 2	
196684	32·4	18·0 × 16·4	24 × 2	
196685	32·5	16·6 × 15·7	23 × 2	
196686	33·5	14·4 × 14·2	23 × 2	
196687	47·5	15·9 × 15·3	24 × 2	
196688	55·5	13·4 × 11·4	22 × 2	Margin of calice broken
196689	38·5	15·0 × 14·4	25 × 2	
196690	40·5	15·0 × 12·6	23 × 2	
196691	50·5	16·8	25 × 2	Margin broken in p–t
196613	33·8	14·5 × 14·1	25 × 2	
	30·8	13·8 × 13·6	26 × 2	Composite colony?
196665	33·2	17·2 × 16·0	22 × 2	Quasi-colony?

* Some corallites may be solitary. Most have proximal parts largely broken. See Table 4 for explanation of abbreviations.

TABLE 3. Colonies more advanced in astogeny.

Specimen number	Length	Generation	Diameter of		Number of septa	Remarks
			Firstly offset pc	Calice		
196680	29·5	pc	4·0 × 3·0	12·0 × 11·0*	25 × 2	Without calice
	10·0	a		8·2	20 × 2	Partly broken
	24·5	a^1		11·6 × 11·2*	25 × 2	Without calice
	8·5	a^2		8·4 × 7·2*	21 × 2	Without calice
	5·0	a^{2a}		5·0 × 5·0*	17 × 2	Without calice
196590	21·0	pc	4·5 × 3·5	12·8 × 12·6	25 × 2	
	26·0	a		14·6 × 12·4	26 × 2	
	12·5	a_1		11·6 × 10·0	19 × 2	Not offsetting
	12·5	a_2		11·4 × 10·2	20 × 2	Not offsetting
	11·5	a_3		11·8 × 7·6	19 × 2	Not offsetting
	25·0	b		15·3 × 11·7	23 × 2	
	11·5	b_1		12·0 × 8·0	22 × 2	Not offsetting
196634	48·7	pc	?6·5	19·4 × 18·2	26 × 2	Beneath calice
	32·5	a		16·4 × 10·0	23 × 2	
	10·0	a_1		11·6 × 10·8	21 × 2	Not offsetting
	16·5	a_2		10·2 × 10·0	21 × 2	Not offsetting
	14·0	a^1		12·0 × 9·2	21–22 × 2	Not offsetting
196645	35·5	pc	?	16·0 × 16·0	26 × 2	
	45·5	a		16·8 × 16·2	?	Max. diameter
				13·8 × 12·7	24 × 2	Rejuvenescence
	23·0	a_1		12·6 × 11·4	22 × 2	Not offsetting
	23·5	a^1		13·1 × 10·3	21 × 2	
	21·5	a^{1a}		14·2 × 12·6	21 × 2	Not offsetting
	16·0	a^2		11·7 × 11·1	21 × 2	Not offsetting
196676	29·0	pc	?6·5	16·2	27 × 2	Broken in p–t
	25·0	a		14·4	26 × 2	Broken in p–t
	23·5	a_1		8·8 × 8·0*	21 × 2	?Not offsetting
	21·5	a_2		12·3	21 × 2	Broken in p–t
	17·0	a_2^1		11·2 × 8·0	20 × 2	Not offsetting
	13·5	a^1		12·4 × 11·2*	22 × 2	
	16·0	b^1		12·8 × 11·0	22 × 2	
	19·0	c^1		9·7*	21–22 × 2	
196621	Protocorallite in calicular part and corallite ‘a’ covered and strangled by descent					
	17·5	pc	?6·0	≈12·5	?	
	30·0	a_1		16·0 × 15·0	26 × 2	
	20·0	a_1^1		13·0 × 12·0*	24 × 2	
	14·5	a_1^{1a}		9·8 × 9·0*	21–22 × 2	Not offsetting
	14·0	a_1^{1b}		8·2 × 7·0*	20 × 2	Not offsetting
	?	a_2		12·6 × 11·8*	27 × 2	
	14·0	a_2^1		10·4 × 9·0*	22 × 2	Not offsetting
	10·0	a_2^2		10·0 × 9·0*	22 × 2	Not offsetting
	10·0	a^1		8·0*	22 × 2	Broken in p–t
	8·0	a^{1a}		7·6 × 5·6	21 × 2	Not offsetting
196678	28·0	pc	?	13·2 × 12·0	22 × 2	
	16·5	a		6·6*	19–20 × 2	
	15·0	b		12·0 × 11·0*	19 × 2	
	23·0	?c		12·0*	22 × 2	
	9·0	?c_1		9·8 × 9·0*	18 × 2	
	10·0	?c_2		10·2 × 9·0*	22 × 2	
	12·0	a^1		10·2 × 10·0*	19 × 2	
	16·0	b^1		11·2 × 9·0*	19 × 2	

* Uppermost margin of a calice is broken. See Table 4 for explanation of abbreviations.

Probably only later generations and, as observed here, only randomly a second asexual generation, started to produce offsets when in a fully mature morphological stage. Unfortunately there are no large colonies in the collection and no further observations of advanced astogeny are possible.

The morphological maturity of asexually produced polyps, similarly to that of protopolyps and their protocorallites, is not automatically correlated with capacity to produce offsets. In general it seems to be dependent on the generation of offsets to which the particular individual belongs, or at least to the stage of astogeny (early or late). In the same way as for protocorallites, the morphological maturity of other corallites should be distinguished from the capacity of their polyps to produce offsets. This is especially important in early stages of astogeny.

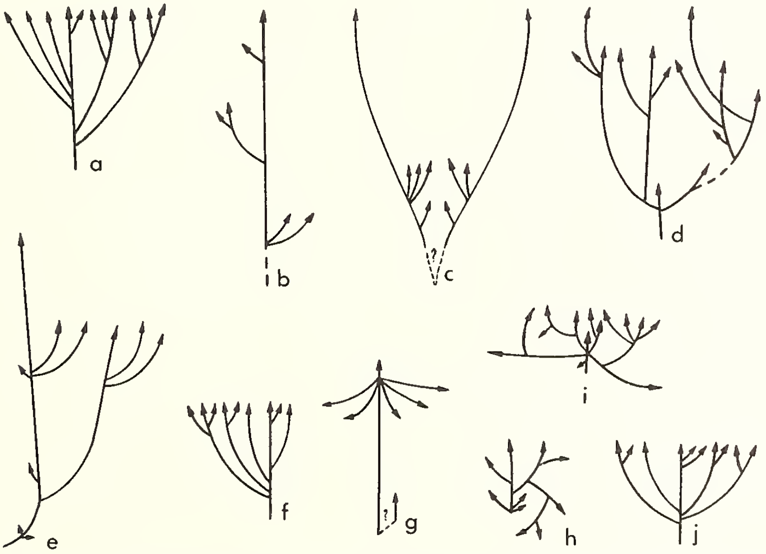
Ulitina (1974) reached a different conclusion regarding measurements of corallites produced at different stages of astogeny. According to her studies of *Hexagonaria philomena* Glinski, there is no difference between corallites within the colony as far as astogenetic stage is concerned. She did not state, however, whether the specimens were measured exactly at the level of offsetting. This would make a fundamental difference, since all corallites observed in the present study continue to increase their dimensions after producing offsets.

Growth and pattern of fasciculate colonies

Fasciculate colonies of rugose and tabulate corals, in a broad sense of the term, have a dual character. All mature polyps in such a colony are generally completely separated from one another. Coates and Oliver (1973, p. 11) stated that particular polyps in such colonies '. . . are in every way similar to solitary corals except that they occupy the numerous extremities on one skeleton (corallum)'. This statement may lead to misinterpretation as corallites of no colony are 'in every way' similar to solitary corals, since the latter have a differentiated genetic code. However, the same authors (1973, p. 4) clarified their point in defining a colony as '. . . a group of individuals, structurally bound together in varying degrees of skeletal and physiological integration, *all genetically linked by descent from a single founding* individual' (my italics). If the stressed phrase in this definition is restated as '*all the asexually produced corallites are diploid and all possess the same fixed genetic code*', then the fundamental difference between separate corallites of fasciculate colony and solitary corals becomes more obvious. Any fasciculate colony should be regarded as a genetic unit which, as a whole, and only as a whole, may be compared with a solitary coral.

Astogenetic studies on graptolites (e.g. Urbanek 1960, 1966, 1973) and hydrozoans (e.g. Schenk 1965) show the very important, leading role of the sexually produced, founding individual of the colony. The morphogenetically active substances (Urbanek's 1966 term) produced by this individual stimulated growth and shape of the colony and of particular asexually produced individuals. In all these colonies, however, the first sexually produced individual is permanently connected with the rest of the colony. This is not so in the material discussed here or in any other fasciculate colonies of rugosans in which all individuals are completely separated. Neither stimulative activity of the first individual, nor any common and directly controlled colony activity can be considered, and all the common actions of a colony must be explained in a different way. The members of the colonies are genetically identical, however, and as such should possess the same tendency for growth of offsetting, and as a result, of pattern. In fact there are obvious regularities in tiny details of offsetting, but one can hardly find any in patterns, apart from the synchronic offsetting discussed below. In my opinion it is almost impossible to indicate any genus or species of rugose corals which produce fasciculate colonies according to a constant scheme, although there are such colonies among Tabulata (e.g. *Halysites* or Auloporidae). However, the question of a direct connection of polyps, especially in Auloporidae, appears to be an open one. In the case when polyps are united, the regularity of such colonies may be discussed using the categories employed for graptolites and hydrozoans.

Oliver (1968) illustrated some patterns in fasciculate colonies and discussed the importance of this character. He stated (p. 21) that 'In most colonies, however, the general pattern is consistent, at least after the initial few generations of offsets', but he also considered (p. 22) that the similarities of patterns of initial growth of some massive colonies '. . . probably represent a generalized pattern characteristic of corals forming massive coralla through lateral increase'. Not even such a weak regularity has been observed in the material described here, and particular colonies start to grow in many ways (text-fig. 4). It can only be stated that no symmetrical and/or exactly simultaneous production of two or more offsets is observed in the



TEXT-FIG. 4. Examples of patterns in colonies of *Heritschioides* sp. nov.; *a*, USNM 196618 and *f*, USNM 196668—asymmetrical colonies; *b*, USNM 196627—quasi-colony; *c*, USNM 196613—most probably composite colony composed of two quasi-colonies; *d*, USNM 196667—dendroid colony tending to chain-like arrangement; *e*, USNM 196634—asymmetrical, simple colony, intermediate between normal and quasi-colony; *g*, USNM 196615—umbrelliform arrangement of offsets; the lowermost, separated corallite may be an attached specimen; *h*, USNM 196635—circumrotary colony; *i*, USNM 196621—chain-like colony overturned in early astogeny; *j*, USNM 196616—symmetrical colony.

protocorallites, although the influence of the substrate may lead to such an impression (Pl. 15, fig. 12*b*; Pl. 16, figs. 4*c*, 6*a*).

The patterns observed in *Heritschioides* sp. nov. may easily be compared with Oliver's (1968) text-fig. 2, C–E, G, and there are also more types present (text-fig. 4 herein). This diversity of pattern of young colonies of one species, and their connection in some cases with extrinsic factors, makes it probable that this is not a genetically fixed taxonomic character, apart from a very general predisposition to produce a given type of colony (e.g. dendroid, phaceloid, etc.). In more variable species, as in the example described here, this predisposition is absent. The enormous variability of pattern and growth form makes it obvious that there was no gene determining a common colony pattern for the species.

Some of the diagrams in text-fig. 4 illustrate an obvious and strong influence of extrinsic factors on colony pattern. Rotary offsetting (text-fig. 4*h*) or asymmetrically umbelliform offsetting (text-fig. 4*g*) resulted from current action which either rolled the colony on the substrate or was directed from only one side. In the latter case a protocorallite may have survived, but it stopped growing (Pl. 17, fig. 4*a*, *b*). Some cases of symmetry or asymmetry (text-fig. 4*a*, *f*, *j*) are related to the substrate on which the young colony developed. A large attachment surface indicates that the colony encrusted the bottom during a young stage of development (Pl. 16, fig. 4*c*).

One phenomenon—cyclic or synchronic offsetting—has to be emphasized, as it is directly connected with pattern, and may also be conditioned genetically. Bulman (1955, 1958) and Urbanek (1973) discussed regularity of branching pattern of some graptolite colonies in which a cyclic and simultaneous branching is observed. This seems to be obvious in the light of Urbanek's (1960, 1966) studies on the leading role of a siculozooid. Nothing like that is possible, however, in fasciculate colonies with completely disconnected corallites. But, as emphasized above, all corallites within the colony possess the same fixed genetic code, and the colony must be treated as a unit. If this is so, one can observe similar reactions of members of a colony to similar extrinsic factors. The cyclic or/and synchronic offsetting observed within the colonies studied here seems to be an example of this type of reaction (Pl. 17, figs. 3, 5*a*, *b*, 6, 7, 8*a*, *b*; Pl. 18, fig. 2*a*).

Ulitina (1974) reported interesting observations on cerioid colonies of *Hexagonaria*, in which, apart from a regular, lateral offsetting in the central area of the colony there is a peripheral offsetting in corallites located on the periphery. The parent, as in most known examples of peripheral increase, died at an early stage of hystero-ontogeny. This may indicate that the reaction of a colony to extrinsic factors is not equal throughout. This requires further investigation to establish whether the environment affects the peripheral corallites more strongly, or whether they are supported to a lesser degree by the colony community. These, and some other factors, may act together.

Spassky and Kravtsov (1974) emphasized growth and patterns of colonies as highly important features in systematics. They followed Spassky's (1965) theory that all rugosans had been divided in their early evolution into two main branches: Solitaria (= solitary corals) and Associata (= colonial corals). These two branches are supposed to have developed independently and parallel to one another throughout the history of rugosans. Many examples (e.g. the families Phillipsastraeaidea, Aulophyllidae, Waagenophyllidae, as well as all the known orders) show that this division is artificial, and that higher taxonomic units (starting from families) contain closely related solitary and colonial corals. The species discussed here is a good demonstration of this artificiality. It includes not only different forms of colonies, but also different forms of growth, both solitary and colonial.

According to the further subdivision proposed by Spassky and Kravtsov (1974, Table 2) the types of colonies and reproduction within rugosan genera and families should be very constant. This is correct in quite a few genera, but it cannot be generalized. As stated above, types of colonies and their patterns appear to be as variable as any other character in Rugosa and particular genera have to be treated individually. These features seem to be of no use for most families and for almost all higher taxonomic units, and neither are the type of reproduction (sexual–asexual), type of coloniality (real colonies–'pseudo-colonies' in Spassky and Kravtsov's sense) and form of growth (solitary–colonial). The history of rugose coral evolution is full of examples of closely related solitary and colonial genera, or fasciculate and massive colonies in the same family.

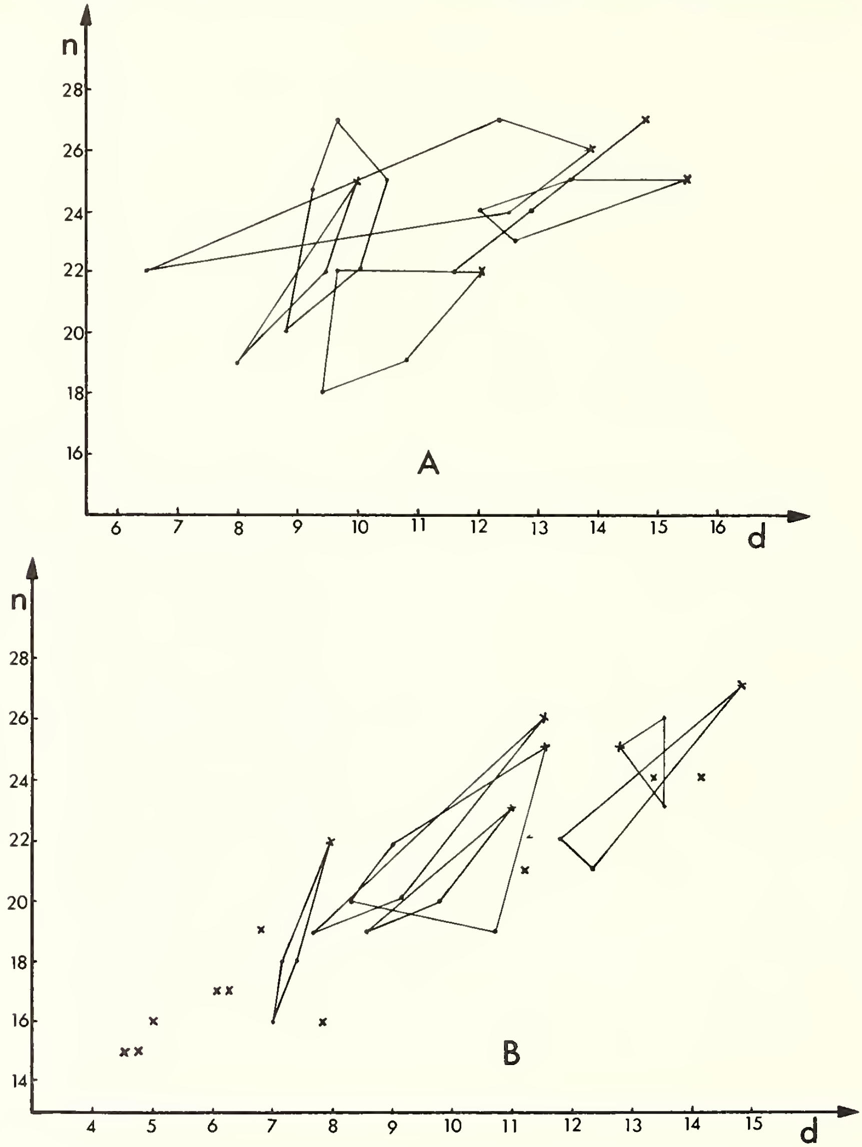
Intercolony variation

The following discussion is limited because the collection consists mainly of well-preserved but astogenetically young colonies. The number of samples analysed is limited to twenty-one, and only protocorallites and the first three asexual generations have been used in constructing text-fig. 5. All colonies analysed show the following common features: 1, a rapid increase of septa with small differences of corallite diameter; and 2, a grouping of corallites of particular generations at similar levels in the diagram.

Intercolony variability, especially in the ratio n/d, seems to be much more important than the similarities noted immediately above. Some colonies have a constant n/d ratio giving a very narrow, almost linear pattern, while some others show widely scattered points corresponding with particular corallites. There are also considerable differences both in the position of particular colonies and the directions of their resultants (text-fig. 5). In contrast to earlier observations (Oliver 1968), intercolony variability of the n/d ratio in *Heritschioides* sp. nov. is so significant that this character possesses almost no taxonomic value. Unfortunately the absence of large colonies makes it impossible to establish the degree to which this variability persists in later astogeny. Comparable measurements of some sub-cylindrical corallites (Table 2) indicate that it may be considerable.

COMPOSITE COLONIES

Composite colonies are those in which at least two protocorallites began to grow so closely to each other that their coralla seem to belong to one colony. They have been described previously only in fasciculate forms (Oliver 1968). According to Oliver composite colonies show distinct differences in measurements between corallites descended from different protocorallites. The n/d ratio was even selected as the best criterion on which to distinguish the composite colony from the regular one. In the collection studied here the differences between corallites descendent from different protocorallites are not much greater than those among the products of the same protocorallites (Table 4). There may be two reasons for this disagreement: 1, Oliver (1968) selected for his study astogenetically advanced colonies with cylindrical corallites, while my study involves a sampling of small, astogenetically young



TEXT-FIG. 5. Ratios of 'n' (number of septa) to 'd' (diameter of corallite in mm). Points corresponding with individual corallites of the same colonies are separately contoured to show the ratios within colonies and their interrelations in species. Protocorallites of individual colonies and those which only started to produce first offsets (diagram B) are marked by crosses. A—n/d ratio measured beneath calices. B—n/d ratio measured close to margins of calices.

TABLE 4. Composite colonies

Specimen number	Length	Generation	Diameter of		Number of septa	Remarks
			Firstly offset pc	Calice		
196619	10·5	pc—1	3·2×4·2	?	18×2*	Incomplete
	23·5	a		10·4× 8·6	20×2	
	37·0	b		11·2×10·2	25×2	
	33·0	b_1		11·0× 7·5	21×2	
	16·5	b_1^1		11·5× 8·7	25×2	
	16·5	b_1^1		11·4×10·4	27×2	
	32·5	c		11·5× 8·2	22×2	
	19·0	c_1		10·4× 8·2	21×2	Not offsetting
	12·0	c_2		8·2× 7·3	19×2	Not offsetting
	9·5	c_3		8·0× 5·6	19×2	Not offsetting
	35·0	pc—2		11·2×11·0	20×2*	
	33·5	pc—3		12·0×10·0	22×2*	
196620	20·6	pc—1		15·6×13·0	23×2	
	26·0	a		14·2×13·6	21×2	Not offsetting
	22·5	b		10·4×10·2	20×2	Not offsetting
	15·0	c		8·7× 8·3	18—19×2	Not offsetting
	11·0	d		9·2× 7·0	18—19×2	Not offsetting
	12·0	e		8·4	19×2	Not offsetting
	26·0	pc—2		14·4×12·0	21×2	One lost structure
196662	14·5	pc—1	≈6·5	10·5× 7·0	22×2	
	16·0	pc—2	≈6·5	9·0× 6·8	20×2	
	6·3	a		8·0× 7·2	20×2	Not offsetting
	3·0	b		7·8× 7·0	18×2	Juvenile
196658	20·5	pc—1		12·8× 8·6	28×2	
	?	a		10·0× 7·0	22×2	
	?	b		9·4× 8·6	20×2	
	?	c		9·4× 9·4	20×2	
	?	c_1		5·5× 4·5	14×2	Juvenile
	?	c_2		5·3× 4·9	17×2	Juvenile
	?	a^1		9·0× 9·0	21×2	Not offsetting
	?	b^1		8·0× 6·6	17×2	Not offsetting
	?	c^1		8·6× 7·0	20×2	Not offsetting
	16·5	pc—2		10·5× 9·1	28×2	

Explanation of symbols

pc—protocorallite.

a, b, c . . . A first ring of offsets produced by a protocorallite.

$a^1, b^1, c^1 \ldots$
$a^2, b^2, c^2 \ldots$
etc. } Next rings of offsets produced by a protocorallite.

$a_{1,2,3\ldots}\ b_{1,2,3\ldots}$
$a_1^{1,2,3\ldots}\ b_1^{1,2,3\ldots}$
$a_1^{1a,b,c\ldots}\ b_1^{1a,b,c\ldots}$
etc. } Second, third, fourth, etc., asexually produced generations of offsets coming from a first ring of offsets of a protocorallite.

$a^{1a,b\ldots}\ b^{1a,b\ldots}$
$a^{2a,b\ldots}\ b^{2a,b\ldots}$
etc. } A first asexually produced generation of offsets coming from second and next rings of offsets of a protocorallite.

colonies. This may overemphasize the differences. However, no other observations are available for comparison. 2, species studied by Oliver are constant in their dimensions, while my material is variable.

As with the dimensions, the morphology of corallites in composite colonies does not vary more than in regular, single colonies (Pl. 17, fig. 2; Pl. 18, figs. 1*a*, *b*, 2*a*, *b*; Pl. 23, figs. 1*a*, *b*, 4*b*, 5*b*). In all my observed composite colonies, only one of the protocorallites produces most of the offsets and, as a result, only one colony is well developed, while the other (or others) is weaker. There are also no offsetting corallites of the same species accompanying the colonies (Pl. 18, figs. 1*b*, 2*b*). In some composite colonies a synchronic offsetting of different components is observed (P. 23, figs. 1, 5). This may emphasize the importance of extrinsic factors in forcing polyps to produce offsets.

PSEUDO-OFFSETS AND PSEUDO-COLONIES

The material under study provides additional examples of phenomena connected with coloniality. A larva might have settled and produced a new polyp between the septa of a dead corallum of the same species that remained in its life position. The skeleton of the new coral grew quite rapidly, filling the interseptal space of the dead corallite and overgrowing some of its septa. It may happen that the cardinal and counter septa of the young corallite form a line directed towards the centre of the 'host' corallite, exactly as during blastogeny (Pl. 23, fig. 6). Two other corallites with the same type of pseudo-offsets, but more advanced in ontogeny are shown on Plate 23, fig. 8. There are also some corallites that show more obviously their pseudo-offsetting relationship (Pl. 23, fig. 3). In this case the larva settled on the calice margin of a 'host' corallite and produced a corallum which overgrew the dead corallite margin from both sides.

The phenomenon of pseudocoloniality may appear in a situation where either a few or many larvae (especially when short-lived), settled together and produced a cluster of solitary corallites growing so closely to one another that the circular shape

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EXPLANATION OF PLATE 23

Fig. 1. USNM 196658, × 1·5. Young composite colony. Both protocorallites produce offsets. *a*, calicular view; *b*, side view.

Fig. 2. USNM 196659, × 3. Young composite colony. Only one protocorallite produces offsets.

Fig. 3. USNM 196660, × 1·5. Pseudo-offset.

Fig. 4. USNM 196661, × 1·5; *a*, *b*, three young corallites attached to each other, growing in different directions to form pseudo-colony.

Fig. 5. USNM 196662, × 1·5. Composite colony. *a*, side view; *b*, calicular view.

Fig. 6. USNM 196663, × 3. Pseudo-offset. A young corallite started to grow between septa of the dead one.

Fig. 7. USNM 196581, × 4·5. Lost structure (see also Pl. 14, fig. 7 and Pl. 15, fig. 14).

Fig. 8. USNM 196664, × 1·5. Well-developed pseudo-offset.

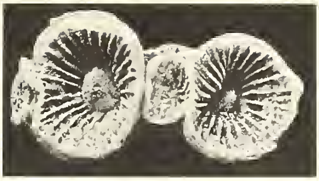
Fig. 9. USNM 196665, × 1·5. Probable quasi-colony.

Fig. 10. USNM 196666, × 1·5. *a*, *b*, pseudo-colony with very strong talon in upper part of one of corallites.

Fig. 11. USNM 196612, × 3. Lost structure (see also Pl. 17, fig. 1*a*–*d*).

Fig. 12. USNM 196628, × 3. Lower part of quasi-colony showing lost structures (see also Pl. 20, fig. 1).

PLATE 23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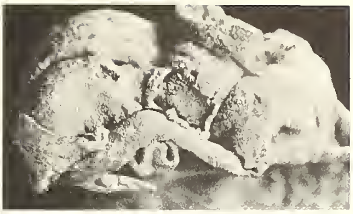
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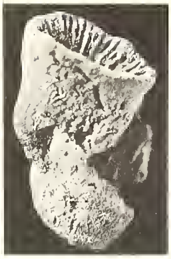
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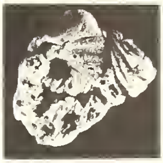
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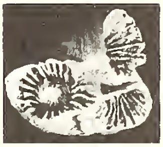
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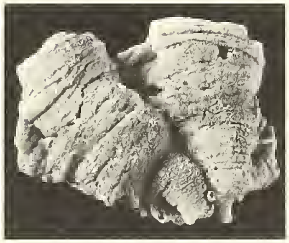
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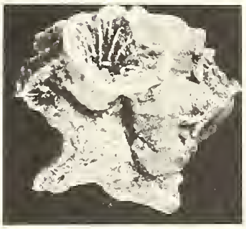
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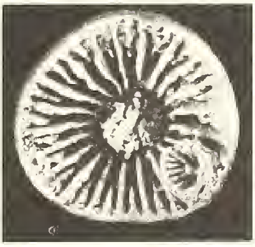
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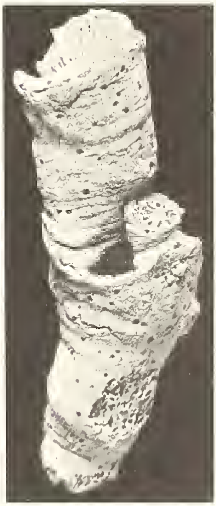
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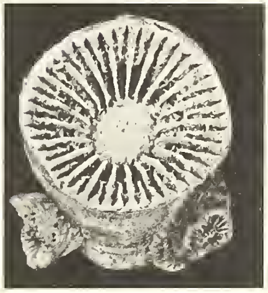
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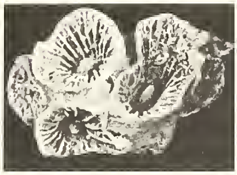
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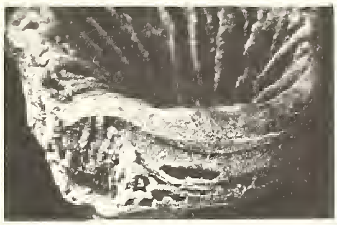
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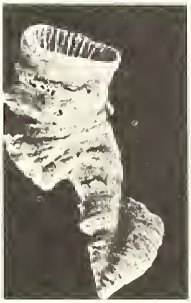
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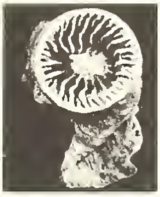
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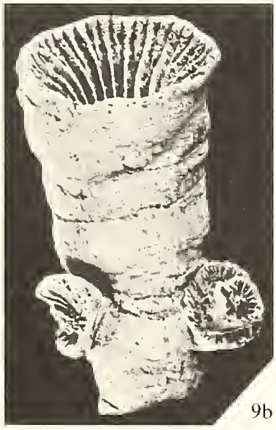
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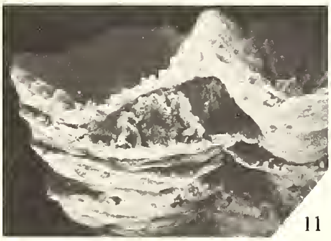
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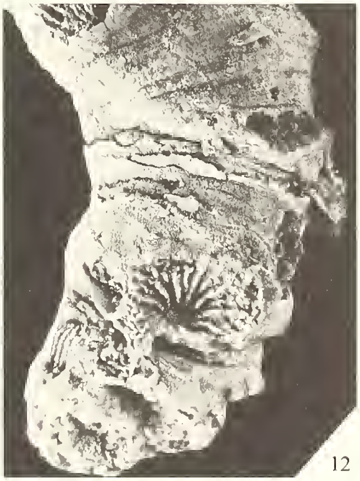
12

FEDOROWSKI, coloniality in rugose corals

of calices became distorted by crowding. Such a cluster, or a weaker one, may be produced on the external wall of a living or dead specimen of the same species and close to the margin of its calice. This gives the impression of a colony with the large corallite being the parent. Such pseudocolonies have been described previously by Fedorowski (1971) from serial sections. Similar examples in *Heritschioides* sp. nov. are observed mainly on young corallites of this generally colonial species, and as such may be regarded as potential composite colonies (Pl. 23, fig. 4*a*, *b*). Sometimes a cluster of larvae settled on a dead corallite calyx (Pl. 21, fig. 7). Corallites produced by these larvae either remained solitary or created weak colonies similar to quasicolonies.

GROWTH OF RUGOSE CORALS

Discussion of the growth of polyps and their skeletons has been renewed recently by Weyer (1972), who did not agree with Wedekind's (1937) views as recently emended by Wells (1969). Instead, Weyer returned to the conception of von Koch (1896) and Matthai (1914) that the margin of a calice is the only permanently upward growing part of a body and skeleton, while the bottom elements are cut off, together with the soft tissues, each time that a new basal skeletal element is built. This is the so-called 'lack of space' hypothesis of Matthai (1914), according to which a calice is adequate only for those soft parts and organs that are actually in it. There would be no room for the body if the bottom of the polyp were pushed upwards to build new basal skeletal elements. To justify this theory Weyer (1972) discussed a number of examples, e.g. synapticulae in Scleractinia and the axial synapticulae in Calostylidae, the structure of some tabulate corals, the existence of an ostracode shell between dissepiments, and the structure and growth of marginal dissepiments in *Manicina areolata* studied by Sorauf (1970), etc. Since the manner of growth of polyps and their skeletons is integrally connected with blastogeny, the subject is discussed further here.

All speculations on growth in recent synapticulate or other scleractinians are avoided here, as the only satisfactory way to solve the problem is to study the relationship between soft and hard parts in recent examples. There must remain a recognizable part of the soft body just beneath the last basal skeletal element if the body is really cut off, and all stages of living corals are easily available.

The fine structure of marginal dissepiments in *M. areolata* and their manner of growth as reconstructed and discussed by Sorauf (1970, text-fig. 6), in no way supports a supposition that they cut off the underlying soft body. On the contrary, Sorauf (1970, p. 16) agreed with Wells's (1969) interpretation of coral growth. In correspondence (March 1976) Dr. Sorauf wrote:

> I have never seen downward growth of dissepiments. In every specimen I have noted or studied to this date all of them have thickened toward the calyx. Only a primary sheet forms by lateral growth, and then thickening occurs by crystal growth towards the base of the polyp. Even in *Manicina* where I felt I could distinguish a third layer (lower spherulitic), it was not developed at or near the junction line where the primary layer joined to complete the first blister.

The presence of an ostracode shell between two dissepiments may be added to by a few other reported observations of foreign bodies embedded in corallite skeletons (see Oliver 1975). These very restricted records argue spectacularly against the theory of cutting off the bottom body in polyps. If this manner of growth had existed there would be many more examples of incorporation of foreign bodies, such as shells of eaten creatures, grains of sand, etc., all of which would have been covered over and incorporated in the skeleton.

The 'lack of space' in the calice would be an argument in a case where a simultaneous and rapid separation of a complete body from a skeleton were proved. However, no evidence for that is retained in the skeleton of rugosans. On the contrary, any longitudinal section clearly shows that particular basal elements of a corallite are connected to the underlying and neighbouring elements in a manner indicating their gradual and individual appearance. The particular elements appear axially from the margin of the calice (text-fig. 2B). Only a very limited extra space is needed in a calice when particular basal skeletal elements appear individually. Additional space is provided continuously by the upward-growing peripheral wall of the calice. This excess of space in calices was one of the bases for Hill's (1936) 'mechanical' theory of growth in corals.

The structure of the Calostylidae and of some Tabulata (e.g. *Cleistopora*, *Donetzites*, *Yavorskia*) does not prove the 'cut-off' theory. Preparation of longitudinal serial sections through such corals for detailed study of the fine structure, would be the only basis to study this. Such a study has not been made, and was not possible here because of lack of material. A body could have been drawn out from any apparently closed skeletal trap as seen in only one section, through an opening not seen in that section. To prove that the medial line of a skeletal trap (if septal in structure) is connected throughout its circumference would be the only possible way to be sure that the soft body was really cut off. The existence of tabulae does not prove this, as they may easily close exits of skeletal traps after evacuation of a body.

Some additional observations are also opposed to the 'cut-off' theory. Most basal elements in Rugosa are convex. This situation may exist only when the soft body, which secretes the skeleton, is supported by something before the skeleton is available. A compressed gas may be this supporting force. It may be replaced later by water, which is in agreement with observations that the spaces between skeletal elements are often filled with water. The presence of a convex and unsupported soft body would be mechanically possible only if it were much lighter than water, but this has never been proved. The 'cut-off' theory also does not explain what happens to mesenteries when the basal part of a polyp is cut off, or how the new basal skeletal elements are attached to the underlying structures which are still covered by soft parts.

Rejuvenescence appears to be important in proving that there is no soft body left beneath basal structural elements. Detailed study of serial sections (Fedorowski 1965*b*) and observations here on etched material show that the process of separation of the soft body from the skeleton begins close to the bottom of the calice. Deep rejuvenescence may repeat a considerable part of ontogeny (Fedorowski 1965*b*, text-fig. 2). The separation is translocated up to the margin of the calice and it includes contemporary basal elements and septa, as is easily seen on etched specimens (Pl. 22, figs. 10*c*, 11). The newly built wall is convex outward and downward. It hangs on septa or attaches to them as a regular wall (Pl. 22, figs. 10*c*, 11). It would be impossible to explain such a construction and interconnections of a new wall, septa, and basal elements if any of these structures were not covered by a soft body. This example shows that the soft body is not differentiated according to the structural element that it builds, and that it goes through the same processes on septa and on basal skeletal elements. It also shows that the polyp may be compressed very considerably if necessary, so that the lack of space in a calice is not a factor. There is no need to look for separate explanations of regular growth and rejuvenescence. The difference is not a matter of quality but of degree of the same factors acting in both cases.

The overgrowth of channels (Pl. 22, figs. 5, 6*c*; text-fig. 2A) as described here also shows that this is a step-by-step process leading to a meeting of an uppermost dissepiment with an upper part of a bridged channel. This is so even in the case of lost structures retained by a parent corallite. The plates overgrowing pores in Tabulata (von Schouppé and Oekentorp 1974) belong in the same category. To construct a new tabula above a pore or above a bridged channel, and to cut off the underlying body seems to be the simplest way of separating two polyps, but this is not the observed case and a special plate is secreted to close the pores or there is special construction of dissepiment-like structures to close the channels. Both these structures are connected to the underlying elements in the same manner as observed in the development of regular basal structures.

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Cover. Reconstruction of the fertile apex of the lycopod-like plant *Asteroxylon mackiei*, from the Lower Devonian Rhynie Chert, Aberdeenshire, Scotland, × 5. The model was made for the Royal Scottish Museum, Edinburgh, by Joyce Collard of H. R. Studios following a reconstruction by W. G. Chaloner, based on photographs by G. Lyon. The photograph comes from a forthcoming booklet by W. G. Chaloner on early land plants, to be published for the Royal Scottish Museum.

CHARLES LYELL'S DREAM OF A STATISTICAL PALAEONTOLOGY

by M. J. S. RUDWICK

Twentieth Annual Address, delivered 16 March 1977

ABSTRACT. The terms *Eocene*, *Miocene*, and *Pliocene* were first used in 1833 in Charles Lyell's analysis of Cainozoic earth-history. Their original meaning and intention in Lyell's mind is here reconstructed, against the background of other contemporary research on the Tertiary strata. Lyell's terms were not originally intended to define contiguous periods of geological time: instead they defined relatively short isolated 'moments', randomly preserved from a far longer span of time. The ages of these 'moments' of preserved time were thought to be determinable in quantitative terms (however approximate and uncalibrated), by reference to the percentage of extant molluscan species that each group of strata contained. This palaeontological 'chronometer' depended on a biological theory of the continuous piecemeal formation and extinction of species at a uniform rate. Lyell originally hoped that his 'chronometer' could be extended backwards beyond the Tertiary and into even earlier periods. Although this ambitious project soon failed, it is conceptually important as an early attempt to use palaeontology to make a general quantitative time-scale for geology.

THE name of Charles Lyell (1797–1875) is well known to geologists and palaeontologists for at least two reasons: he is widely considered a pioneer of so-called 'uniformitarianism' in the earth sciences; and he is remembered as the originator of the terms Eocene, Miocene, and Pliocene, which even in the modern era of radiometric dating still dominate the descriptive stratigraphy of the Cainozoic (for historical re-evaluations of 'uniformitarianism', see Hooykaas 1959; Cannon 1960*a*; Rudwick 1971). This paper aims to show that Lyell's stratigraphical terms are 'conceptual fossils'; they are fragmentary relics of an ambitious theoretical project in stratigraphical palaeontology. This project faltered and failed almost as soon as it was launched, and the stratigraphical terms were 'metamorphosed' almost out of recognition. But Lyell's project is worth reconstructing none the less, because it serves to tie his practical work in applied palaeontology firmly into his broader programme for research on all aspects of the earth sciences.

Lyell himself had few personal followers and founded no distinct 'school' or research tradition. But it is difficult to over-estimate the influence of his compendious *Principles of geology* (1830–1833) and its later offshoot the *Elements of geology* (1838), which were widely translated and repeatedly updated in successive editions through nearly half a century. Lyell's persuasive interpretations of the accumulating empirical research of the mid nineteenth century were absorbed, selectively but pervasively, into the thinking of the first generations of professionalized geologists and palaeontologists; and his general approach has remained an essential element of the 'taken-for-granted' tacit knowledge of earth scientists to the present day.

THE PROBLEM OF THE TERTIARY FAUNAS

It is no accident that Lyell's permanent legacy to stratigraphical terminology should concern the Tertiary strata ('Tertiary' was used to cover all the 'Cainozoic' of modern

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geology except what were later interpreted as glacial and post-glacial deposits). This was not, however, because he sought to make an original 'contribution' by specializing in an 'under-developed' research field. Yet when Lyell first entered the community of active geologists centred on the Geological Society of London (Morrell 1976), Tertiary stratigraphy was in a certain sense under-developed. If the term 'paradigm' is used with proper caution in its historical sense (Kuhn 1962, *not* the palaeontological sense of Rudwick 1961, etc.) to describe a dominant style of research in a particular science at a certain period, then stratigraphy around 1830 was developing with great rapidity and success by following a paradigm that was primarily 'structural' in its cognitive goal (Rudwick 1976*b*) and increasingly palaeontological in its method. In other words, attention was focused on the discovery of the correct order of succession of formations, seen as a problem of three-dimensional structure; while 'characteristic fossils' were being used with increasing confidence as the most reliable (though not the only) criterion for the correlation of formations in different regions. The first aspect reached back to the highly fruitful research tradition of Werner and his followers (Ospovat 1969); the second aspect, while not altogether original to William Smith (1769–1839), certainly gained increasing emphasis from the manifest value of Smith's great geological map and its palaeontological illustrations (Smith 1815*a*, *b*; 1816–1819).

This paradigm was centred, however, on the strata with which Smith himself had had his greatest success: the so-called 'Secondary' formations (roughly equivalent to the Mesozoic and Upper Palaeozoic of modern geology). These could be divided relatively easily into formations of distinct and diverse character, many of them containing equally distinct and diverse fossils in some abundance. Below the Secondary strata, however, were the confusing 'Transition' strata and 'Primary' rocks (in modern terms, pre-Carboniferous strata and many metamorphic and igneous rocks), often highly disturbed and with few if any fossils. Above the Secondary strata were the Tertiary, which often seemed almost equally confusing, though for different reasons.

The Tertiary strata had indeed provided the paradigm of stratigraphy with an 'exemplar' that was at least as influential as Smith's, namely the study of the Paris region by Georges Cuvier (1769–1832) and Alexandre Brongniart (1770–1847). Their work showed the possibility of identifying a series of distinct formations over a wide area, using characteristic fossils as a tool of major importance; and their results were actually available in published form before Smith's (Cuvier and Brongniart 1808; 1811). But it soon seemed as if the Tertiary formations differed rather fundamentally from the Secondary. Tertiary strata seemed always to be confined to scattered 'basins'—the term was used in a quite literal sense, since the sediments were envisaged as having gradually filled pre-existing hollows in the underlying rocks. Cuvier and Brongniart described the Paris basin; Thomas Webster (1773–1844), the draughtsman at the Geological Society of London, soon afterwards described analogous Tertiary strata in the London and Hampshire basins (Webster 1814; 1816); and other basins were quickly added to the list during the 1820s. This apparent contrast between isolated Tertiary basins and widespread Secondary strata was heightened by the fact that the uppermost Secondary formation, namely the Chalk, was the most widespread and most distinctive formation of all.

A further difficulty derived from the very success of the French research. The most striking faunal distinctions among the strata of the Paris basin were given an interpretation that went far beyond the merely structural level of most stratigraphical work, reaching instead for a causal explanation. Using analogies with present-day faunas and floras, Cuvier and Brongniart interpreted the Parisian strata as an alternation of marine and non-marine formations; and a somewhat similar alternation was recognized by Webster in the Hampshire basin. This ecological dimension, coupled with the great difficulty of correlating the formations of one basin with those of another, led to a generally implicit but widespread belief that the Tertiary strata had accumulated under conditions that somehow differed radically from the Secondary.

This belief was probably reinforced by the analogous but even greater problems surrounding the most 'superficial' deposits of all. The unconsolidated, highly irregular, and often peculiar deposits that are now interpreted as glacial and post-glacial seemed naturally to suggest a major break in geological processes in the relatively recent past. Such an episode was sometimes labelled 'diluvial'; but when links with the biblical Deluge were expressed, this involved no mere literalistic interpretation (e.g. Buckland 1823), and in any case the phenomena themselves seemed to make some kind of drastic causal explanation inescapable (Rudwick 1970*b*; 1972, chapter 3).

At an early stage in his geological career, Lyell became dissatisfied with the prevailing tendency to assume the kinds of causal discontinuity that have just been summarized. It is difficult, however, to judge the relative importance, or mode of interaction, of theoretical and practical components in the development of his outlook. He may have been influenced by John Playfair's (1802) reinterpretation of the 'geological' aspect of the wide-ranging 'natural philosophy' of James Hutton. But since Lyell entered the field of geology in a period of self-consciously rapid development, he might well have found these authors merely 'old-fashioned' (see Porter 1976; 1977). He is likely to have been more impressed by seeing for himself the Tertiary strata around Paris. In 1823 he had as his guide Constant Prévost (1787–1853), who had already argued in public that the ecological explanation of the strata given by Cuvier and Brongniart could be brought even more closely into line with present-day analogies (Prévost 1823).

Lyell's first major scientific paper (Lyell 1826*a*) was devoted to showing that one characteristic Parisian lithology, a freshwater limestone, had a close modern analogue in the lakes near his Scottish family home. In his first essay on geology written for a more general audience (Lyell 1826*b*) Lyell extended this into the suggestion that Cuvier and other illustrious geologists had been premature in concluding that such analogues between present and past could not be found and used for explanation throughout geology. Lyell's confidence in this conclusion was strengthened by a persuasive case-study of the already classic area of Auvergne, published by his friend the political economist George Poulett Scrope (1797–1876) (Scrope 1827; Rudwick 1974). Lyell's review-essay on Scrope's work (Lyell 1827) shows clearly how he was adopting Scrope's picture of the very gradual development of the physical geography of central France, and trying to extend it to incorporate a picture of similar gradual change in its fauna and flora. Lyell explicitly used this example to illustrate how it was unnecessary to postulate sudden events of uncertain character in the past: all the observed phenomena of the Tertiary strata and their fossils could be explained without recourse to such events, simply by reference to processes observable at the present day.

At about this period, Lyell conceived the idea of writing a book that would reorientate geological interpretation along these lines. After many delays, and a change of plan that transformed it from a short elementary introduction into a massive three-volume work, the book was published as the *Principles of geology* (Lyell 1830–1833). Significantly, it was subtitled ‘an attempt to explain the former changes of the earth’s surface, by reference to causes now in operation’. Within this work, Lyell’s reinterpretation of the Tertiary occupied a crucial position (Rudwick 1970*a*). In the first two volumes, Lyell surveyed the varied ‘causes now in operation’ that make for change in both inorganic and organic spheres, arguing that this repertoire of present-day processes was much more varied and more powerful than most other geologists had realized. In the final and culminating volume (1833), these processes were put to work in the causal interpretation of the stratigraphical record. Lyell illustrated this mode of interpretation chiefly by the example of the Tertiary. He chose the Tertiary because it was important for him to demonstrate the validity of his approach for the relatively recent epochs of earth-history. By doing so, he could both eliminate the supposed ‘diluvial’ break between the Tertiary and the present, and also go on to show that the contrast between the Tertiary and the Secondary was merely a difference of degree, not kind.

Within this over-all strategy, Lyell’s concepts of Eocene, Miocene, and Pliocene played a crucial role, but a role that has often been misunderstood. To uncover Lyell’s original intentions in coining these terms, it is necessary to look in more detail at previous interpretations of the Tertiary strata and at the development of Lyell’s own ideas.

In analysing the formation of any novel scientific theory or project, it is important first to survey the range of other relevant theories or projects that were actually available as ‘resources’ that the principal figure under study could have utilized in his own construction. In the present case, at least four such existing pieces of work seem to have been relevant.

Firstly, the already classic description of the Parisian strata by Cuvier and Brongniart (1811) yielded a picture of the gradual accumulation of strata within a single basin under alternately marine and non-marine environmental conditions. Cuvier and Brongniart had given these ecological changes a ‘catastrophist’ interpretation, inferring that they had been caused by sudden changes in physical geography. Yet on Prévost’s reinterpretation (1823) these variable conditions were to be expected, on present-day analogies, in any shallow gulf of the sea near the mouth of a large river. Not only was this the kind of explanation that Lyell intended to deploy more generally, but it also suggested that each Tertiary basin would have to be treated in the first instance as a separate entity. In other words, Lyell probably realized that it would be futile to search for exact correlations between the formations in different basins, if they owed their characteristics to essentially local factors.

A second major ‘resource’ for Lyell was the work of the Italian naturalist Giovanni Battista Brocchi (1772–1826), who had published a superb monograph on the molluscs of what he called the ‘Subappenine’ strata in north Italy, soon after the Parisian strata had been described (Brocchi 1814). It is probable that Lyell was familiar with this work at an early stage in his career: it was still perhaps the best monograph on any Tertiary fauna even ten years after publication. Its Italian was almost certainly no serious barrier to Lyell, since his father was a noted Italianist and he himself knew the language well enough in the 1820s to review a new edition of Danté (Wilson 1972, p. 187); and he also borrowed extensively from Brocchi, with scant acknowledgement, when later he was writing the historical introduction to the *Principles* (McCartney 1976). Brocchi prefaced his systematic work with a very long introduction, which included important interpretative comments on the relationship between his Italian fauna on the one hand and the Parisian and the present-day faunas on the other. Brocchi was a good enough naturalist to be aware of present-day regional faunal variations, and so he attributed the difference between the Subappenine fauna and the Parisian fauna to what we would term biogeographical factors. This was entirely reasonable, since there was no evidence to suggest any difference of age between the two basins. On the other hand, he was also aware that many of his Subappenine species had no living counterparts, and were probably extinct. However, he rejected Cuvier's 'catastrophist' explanation of extinction as inapplicable to marine molluscs—Cuvier had suggested that the extinct Tertiary land mammals had been annihilated by sudden marine incursions—and he found it a superfluous hypothesis anyway. In its place, Brocchi suggested an organismic explanation: species, like individuals, probably have a limited life-span, eventually losing their reproductive vigour and therefore dying out. On this model, extinction would be an essentially piecemeal process. This, he thought, might explain why his Subappenine fauna contained a mixture of extant and apparently extinct species. Furthermore, he pointed out that individuals of different biological groups have life-spans that vary from a few hours to a few centuries (e.g. insects and trees), and he thought that by analogy the average life-spans of species belonging to different groups might also vary widely. This could explain why the Tertiary strata contained many extant molluscan species, whereas their mammalian fossils were apparently all extinct.

Thirdly, Lyell was almost certainly familiar with the first full description of the basin in south-west France, published in 1825 by the young Parisian naturalist Barthélemy de Basterot (1800–1887). This memoir not only added another Tertiary basin to the growing list, but also included an important theoretical interpretation. Basterot derived his analysis explicitly from the new quantitative biogeography of the Swiss botanist August-Pyrame de Candolle (1778–1841). In his celebrated article on 'Géographie botanique', Candolle (1820) had used a wide range of published floras, from all parts of the world, to construct quantitative tables based on the numbers of genera and species common to various areas. These tables enabled him to distinguish twenty major biogeographical regions with distinct indigenous floras. He borrowed the then current meaning of the term 'statistics'—it denoted the collection of quantitative economic data for political use by the 'statist' or statesman—and he called his own work 'statistique végétale'. Basterot applied Candolle's botanical 'statistics' to his own palaeontological problem of the Tertiary molluscan fauna of the Bordeaux region. He had identified a total of 330 species in this fauna, and he analysed them quantitatively in two distinct ways, in relation to living species and in relation to other Tertiary faunas. Of the total number of species, only 45 were known to live in European seas and another 21 elsewhere in the world. Divided the other way, he noted that 91 species were also reported from Italy, 66 from the Paris basin, 24 from England (the Hampshire and London basins were not distinguished), and 18 from the Vienna basin; while 110 appeared to be peculiar to the Bordeaux basin. He suggested on the basis of these figures that the faunal similarity between any two basins might be roughly proportional to their geographical proximity.

Basterot's figures are not even completely consistent, and he did not attempt any more sophisticated analysis of them. His remarks are important, however, because they suggested at least the possibility of giving quantitative or 'statistical' precision to Brocchi's earlier inference that the faunal differences between the various Tertiary basins might reflect a pattern of Tertiary biogeographical factors. In other words, the diversity of the Tertiary faunas might be a function of space, not of time.

The fourth and last major 'resource' for Lyell's construction of his own interpretation of the Tertiary was the work of Scrope (1827), which has been mentioned already. Although Scrope was not concerned at all with the palaeontological aspect, he did describe the Tertiary strata of the Massif Central in enough detail for Lyell to realize that they were exclusively non-marine. More significantly, however, Scrope analysed the long history of the area, and showed that sporadic outbursts of volcanic activity had punctuated the gradual and continuous erosion of the Tertiary sediments. He argued that the lava-flows, isolated by subsequent erosion at various heights, formed 'a natural scale' or chronometer for estimating the relative *age* of the eruptions (Rudwick 1974). In other words, a quantitative measuring device, however approximate and uncalibrated, could be discovered within the geological phenomena themselves, and could convert the appearance of discontinuity into evidence of underlying continuity.

LYELL'S CONSTRUCTION OF A FAUNAL CHRONOMETER

Lyell's construction of his own distinctive theory for the Tertiary faunas, integrating the pre-existing 'resources' that have just been summarized, can be dated to the successive phases of his most important season of geological fieldwork. This was his long expedition through France and Italy in 1828–1829, partly in the company of his friend Roderick Murchison (1792–1871), who was not yet a rival. Lyell's development of his theory, which underlay his later terms Eocene, Miocene, and Pliocene, will be reconstructed here on the basis of the accessible records of his journey, namely his subsequently published letters from this period (K. Lyell 1881, pp. 182–251), some brief published extracts from his notebooks (quoted in Wilson 1972, pp. 187–261, and a few unpublished letters.

Lyell and Murchison first studied the areas that Scrope (1827) had described in the Massif Central. Lyell at least was completely convinced by Scrope's arguments for the very gradual erosion of valleys (Lyell and Murchison 1829*a*), and he must surely have recalled, when seeing the ancient lava-flows with his own eyes, how Scrope had used them as a quantitative 'natural scale' to measure geological time. Certainly he was impressed by the span of time that was implied by the hundreds of feet of thin-bedded Tertiary limestones, which were clearly the product of slow and tranquil deposition. All this confirmed his growing conviction, shared with Scrope, that most other geologists were seriously underestimating the sheer magnitude of geological time.

Lyell's interests, however, were more palaeontological than Scrope's, and he developed Scrope's pattern of interpretation in more biological directions. He checked that the Tertiary strata were indeed all freshwater in origin. Although strikingly similar to some of the Parisian limestones, they were also comparable to modern lake-marls, and contained similar freshwater molluscs and plants. On the other hand, the mammalian fauna of the Massif Central had evidently changed as much as it had in the Paris region, since local naturalists had discovered and described a fine fauna of extinct mammals (Croizet and Jobert 1826–1828; Deveze and Bouillet 1825–1827). But since there was no sign of any marine incursion into the area, Cuvier's explanation of the extinction of similar mammals in the Paris region was clearly invalid for the Massif Central. This may have confirmed Lyell's suspicion that some more gradual cause of extinction must be found. A further indication was that the mammalian fossils had not come from the freshwater limestone formation, but from a much younger—though still 'ancient'—river-gravel (Lyell and Murchison 1829*a*). The area thus contained a relatively recent mammal fauna that was full of extinct species, while the older Tertiary lake-deposits contained freshwater molluscs and plants much closer to those of the present day.

This evidence probably made Lyell recall Brocchi's suggestion that extinction might be caused by the intrinsic 'old age' of individual species, and that species in some groups (such as mammals) might have much shorter 'life-spans' than species in other groups (such as molluscs). Some such speculations along Brocchian lines are strongly suggested by the fact that while he was still in the Massif Central Lyell wrote a short essay in his notebook entitled 'On the laws which regulate the comparative longevity of species' (Wilson 1972, p. 215).

A few weeks later, Lyell and Murchison had left the Massif Central and reached Nice, where Lyell made use of the local knowledge of Giovanni Antonio Risso (1777–1845). He studied a thick Tertiary conglomerate formation and speculated on its causal origin; and he mentioned in a letter home that 'in the intervening laminated sands are numerous perfect shells, more than 200 in Risso's cabinet, 18 in a hundred of which are *living* Mediterranean species, whose habits are known' (K. Lyell 1881, p. 199). Risso himself, in his five-volume description of the natural history of the Nice area, had published long lists of molluscan species from the 'Formation Tertiaire' (Risso 1826, vol. 1, art. 4); but he had not distinguished the extant species among them, and the percentage expression was therefore probably Lyell's own gloss on Risso's work. It is in fact the first hint that Lyell was beginning to apply the quantitative or 'statistical' approach that Basterot had borrowed from Candolle. The context of Lyell's remark suggests, however, that he was using the numerical proportion purely as an ecological criterion, not as an indicator of geological age. The 'habits' of the extant species helped to show that the conglomerate formation had been deposited in conditions differing little from those probably still existing offshore.

After crossing the Appenines, Lyell and Murchison were able to study another important collection at Turin. Here Franco Andrea Bonelli (1784–1830) had already noted the faunal similarity between some of the local strata and Basterot's in south-west France (Wilson 1972, p. 221). Lyell recognized the Turin strata as similar to those he had been studying along the Mediterranean coast. In a letter from Milan shortly afterwards he referred back to 'the sub-Appenine beds from Montpellier to Savona, containing as they do nearly twenty per cent of decided living species of shells' (K. Lyell 1881, p. 201); and the context makes it clear that he was now using that percentage as an indication of *age*. This was because the strata near Turin were highly tilted; and Lyell already suspected from what he had seen in the Massif Central that there was a causal connection between tectonic disturbance and volcanic activity (Lyell and Murchison 1829*b*).

In pursuit of this hypothesis, Lyell left Murchison in northern Italy, and turned south towards Sicily to study active volcanoes, for in their vicinity he explicitly anticipated finding still more recent strata elevated above sea-level. This expectation was duly fulfilled (Wilson 1969; Rudwick 1969); and in the development of his hypothesis of elevation he made increasing use of the proportion of extant species in a fossil fauna as a guide to the relative age of the formation in which it was preserved. Brocchi had died only two years earlier, and so Lyell was denied the chance of a personal discussion with him; but Brocchi's Subappenine fauna, with its mixture of living and extinct species, was clearly playing a key role in Lyell's mind. Furthermore, unlike Basterot and even Brocchi himself, Lyell was now comparing different Tertiary areas primarily in terms of their relative ages, rather than in biogeographical terms. For example, after concluding his fieldwork in Sicily, he told Murchison how the strata he had studied there must be much younger than the Subappenine formation: 'I am come most unwillingly to this conclusion. But the numerous extinct species which characterise the Subapps. are wanting [missing] here, & living shells are present too plentifully, to admit a doubt that it is more related to our own epoch' (K. Lyell 1881, p. 233).

Up to this point, it seems that Lyell was using the proportion of living and extinct species in a purely empirical way and as a purely geological tool. But on his journey back through Italy a meeting with the botanist Domenico Viviani (1772–1840) at Genoa apparently turned his thoughts in a much more biological direction (K. Lyell 1881, p. 243). Lyell was so excited by what he called 'my new geologico-botanical theory' that he crossed the Alps in the depths of winter specially to talk about it with Candolle in Geneva. His report of his discussions with Viviani and Candolle merits quotation at some length.

> I am now convinced that geology is destined to throw upon this curious branch of inquiry [i.e. biogeography], and to receive from it in return, much light, and by their mutual aid we shall very soon solve the grand problem, whether the various living species came into being gradually and singly at insulated spots or centres of creation, *or* in various places at once and at the same time. The latter cannot, I am already persuaded, be maintained. Viviani was puzzled to account for Sicily having so much less than its share of *peculiar* indigenous species; but this [is as it] should be, for *I* can show that three-fourths of this isle [i.e. Sicily] were covered by the sea down to a period when nine-tenths of the present species of shells and corals (and by inference of plants) were already in existence. Such an isle, like Monte Nuovo [the 'new' volcano formed in 1538 near Naples], has been obliged to borrow clothes from its neighbour, having scarcely had time to furnish any yet for its own nakedness. It has not yet seen out a tenth, perhaps not a twentieth part of a revolution in organic life. Give it the antiquity [i.e. as a *land* area] of the high granitic mountains of Corsica, and it will also boast its indigenous unique plants, unknown elsewhere either in the Mediterranean or other part of the globe [K. Lyell 1881, p. 246].

This important passage records the first rough outline in Lyell's mind of a wide-ranging *theory* of organic change, which would integrate evidence from biogeography, palaeontology, stratigraphy, and structural geology.

Like almost all naturalists at this period, Lyell believed that species were real entities, intra-specific variation being often considerable but always finite. There seemed to be good empirical grounds for rejecting Lamarck's earlier postulate of limitless variation.

The problem of accounting for the *origins* of these discrete units was therefore acute. Lyell probably shared the general belief that the production of new species must have been under divine providential control, in order to account for the precise adaptation of each species to the environment in which it was placed. Certainly he expressed this view, probably with complete sincerity, during his first public lectures on geology only three years later (Rudwick 1975; 1976*a*). But in the contemporary understanding of 'providence', such a view was quite compatible with a belief that God could have used some natural process or 'secondary cause' to achieve this end (Cannon 1960*b*). In the passage just quoted, Lyell seems to imply that new species would somehow originate spontaneously, if the appropriate ecological niches were vacant for long enough, as they might have been on an ancient and rather isolated island like Corsica. This process had not yet occurred on Sicily, he thought, because it had emerged from the sea-bed so recently, and it was so close to an existing land-mass that existing species had simply spread to it. The important point about Lyell's speculations, however, is that he clearly envisaged a process of *piecemeal* production of new species, in appropriate ecological situations that would tend to be scattered in both space and time. Also implicit in the quoted passage is Lyell's belief that the extinction of species was a process similarly piecemeal in character. As already mentioned, he had probably derived this idea from Brocchi and he may still have been using Brocchi's notion that the cause of extinction was the 'old age' of each species.

These two processes in conjunction produced an over-all pattern of continuous piecemeal change in the whole fauna and flora. With such a process of organic change, the specific composition of (say) the molluscan fauna, if followed from any given moment in past geological time, would gradually change until all the old species had been replaced by new ones. Lyell referred to such a cycle of change as a 'revolution'. For him this word carried no overtones of sudden violence; he used it in the older but still current sense of a complete cycle, such as the turning of a wheel or the circling of the Earth around the Sun. In the present context it meant a complete turnover in the specific composition of the fauna or flora (of some particular biological group).

This concept of slow cycles of organic change was given a quantitative dimension in Lyell's mind, by being geared to his previously empirical use of the proportion of extant species in various Tertiary molluscan faunas. This now became implicitly a *measure* of geological time. Thus in the passage quoted above, Lyell was measuring the age of Sicily as a land-mass by reference to the mere 5 or 10% of extinct molluscan species in its youngest marine strata; he was saying in effect that this represented an age of only 5 or 10% of one complete turnover or 'revolution', conceived as a major unit of geological time.

In the foregoing interpretation of Lyell's thought, I have made explicit a theoretical structure that was only hinted at in the available documentary record, and my interpretation has been guided by Lyell's own explicit statements of a slightly later date (particularly in the *Principles of geology*). Nevertheless, I believe that there is enough evidence to indicate that by the time he left Geneva early in 1829, Lyell had already constructed a theory of organic change that in principle provided the basis for a faunal chronometer for geological time.

From Brocchi he had drawn the idea of piecemeal extinction, and the notion that the molluscan species had intrinsically longer life-spans than, for example, the more spectacular mammalian species. He had then used Brocchi's emphasis on the mixture of extant and extinct molluscan species in the Subappenine fauna as the basis for a measure of geological age. He had seen the value of Basterot's quantitative comparisons of the faunas of different Tertiary basins; but he had reinterpreted Basterot's (and indeed Brocchi's) comments on these differences, seeing them not as a reflection of biogeographical factors, but primarily as a result of the different geological ages of the basins. Yet he had welcomed the biogeographical insights of Viviani and the great Candolle, integrating their stress on the spatial dimension with his own temporal emphasis, to produce a theory in which the piecemeal production and extinction of species was closely geared to the ever-changing local environment. Finally, he had seen the various Tertiary basins, like Scrope's sporadic lava-flows in Auvergne, as preserved 'moments' in a much longer history, for which a 'natural scale' or chronometer could be constructed.

Having sketched the theory just outlined, Lyell realized that its development required above all a sound knowledge of fossil and living molluscs. On his way back to London he therefore stayed in Paris to learn all he could from one of the best conchologists in Europe, Paul Gérard Deshayes (1797–1875). He was perhaps disappointed, yet also encouraged, to find that both Deshayes and another Parisian naturalist, Jules-Pierre Desnoyers (1800–1887), had independently reached somewhat similar conclusions about the Tertiary strata and their fossils: disappointed, because it might detract from the acclaim he hoped to receive for his work; encouraged, because the independent conclusions of others did at least confirm the validity of his own formulation. Although apparently Lyell did not know it at the time, yet another geologist, the young Heidelberg professor Heinrich Georg Bronn (1800–1862) had also been working on somewhat the same lines.

On the face of it, this looks like a striking case of what some historians and sociologists of science have analysed as 'simultaneous discovery' (e.g. Merton 1957; Kuhn 1959). There is indeed an element of simultaneity, but it is hardly surprising that several naturalists should have been working at the same time on the problem of the Tertiary strata and their fossils. The sheer accumulation of descriptive papers and monographs was making it increasingly evident that the Tertiary was not just a single major formation, but a highly complex series of formations, and this knowledge was readily accessible to the whole European geological community through an already well-developed system of scientific periodicals. Yet beyond this general concern to reduce the Tertiary to greater order and coherence, a detailed comparison of Lyell's work with that of other naturalists greatly reduces the element of coincidence.

Desnoyers had discovered a stratigraphical overlap that proved, by the ordinary principles of superposition, that the Tertiary strata of the Touraine region were younger than those in the Paris basin to the north. Desnoyers (1829) generalized this into a theory of the successive existence and filling of the various Tertiary basins, and used this theory to explain, for example, why the Crag of East Anglia was much closer faunally to the Touraine strata than to the London basin, although it was much further away geographically. For such a case, Desnoyers's view was clearly superior to Basterot's biogeographical explanation. Yet this palaeontological aspect played only a very minor role in Desnoyers's argument; and, furthermore, he attributed the formation of new basins to sudden tectonic events—the kind of interpretation that

Lyell was most concerned to eliminate from geology. So although Desnoyers added a footnote to his article in proof stage (1829, pp. 214–215), expressing his pleasure that Lyell had reached similar conclusions on the successive filling of the Tertiary basins, there was really only a small degree of overlap between their work. In the part of Desnoyers's memoir that he had completed before Lyell's stay in Paris, there is no sign of Lyell's more comprehensive vision of a complex pattern of continuous environmental and organic flux. Desnoyers was there concerned with the more conventional goal of dividing the Tertiary strata into successive *periods* of formation.

Deshayes shared this aim, complementing Desnoyers's stratigraphical fieldwork with a museum-based palaeontological study of Tertiary molluscan faunas. Before Lyell arrived in Paris, Deshayes had apparently already distinguished three groups of Tertiary formations on the basis of their fossils. Yet a detailed analysis of his published conclusions shows that he interpreted these groups of formations in conventional terms as the products of three successive and temporally contiguous periods of geological time. In his first brief announcement of his results, Deshayes (1831*a*) distinguished a first epoch with 3% extant species (e.g. Paris and London basins), a second epoch with 19% extant species (e.g. Basterot's Bordeaux strata and Desnoyers's Touraine strata), and a third epoch with 52% extant species (e.g. Brocchi's Subappenine strata and the English Crag). He referred to these as 'three great zoological epochs, completely distinct by the assemblage of species in each, and by the constant proportions between the number of living species and those that are lost' (Deshayes 1831*a*, p. 186). In fact Deshayes also mentioned a fourth group of strata with 96% extant species (e.g. the most recent of Risso's strata at Nice and Lyell's in Sicily), but he evidently thought these too recent to deserve the rank of 'epoch'. It is therefore clear that Deshayes was using his quantitative faunal analysis to define sharply *distinct* epochs: it was a useful tool for determining the temporal order of formations, in cases where the more conventional criteria of stratigraphical superposition and characteristic fossils happened to fail. In fact this is explicit in his fuller memoir (Deshayes 1831*b*), where he urged selection of characteristic fossils from the larger assemblages in which they occurred, and at various levels of specificity (e.g. '*Lucina divaricata*' for all the Tertiary strata, '*Cardium porulosum*' for the Parisian strata, and '*Cucullea cravatina*' for the lower *Calcaire grossier*). In other words, Deshayes was clearly concerned to use fossil assemblages simply to divide the Tertiary into discrete epochs; formations could then be assigned to the correct epoch by appropriate characteristic fossils, if the criterion of superposition was not available.

This project differed fundamentally from Lyell's in its cognitive goals and structure of thought. But the contrast has been masked by the fact that Lyell paid Deshayes, who badly needed financial support, to supply him with a complete 'statistical' analysis of the Tertiary molluscan faunas, for Lyell to use in the *Principles of geology*. This arrangement necessitated a certain compromise in Lyell's presentation of Deshayes's results.

Before analysing Lyell's use of Deshayes's work and the articulation of his own very different theoretical framework for Tertiary earth-history, a brief comment on Bronn's work is appropriate, although Lyell did not hear of it until later. Bronn toured northern Italy at about the same time as Lyell (though they did not meet), and used many of the same local informants. After his return to Heidelberg he published an elaborate quantitative analysis of the complete fossil record, with a more detailed analysis of the Tertiary faunas of the various European basins (Bronn 1831). Bronn's tables are an outstanding example of the 'statistical' approach in palaeontology at this time (remembering that 'statistics' meant simply a compilation of quantitative data). For each fauna he counted the numbers of genera and species belonging to various major groups, and converted these numbers into decimal fractions for easier comparison. For the Tertiary formations he calculated degrees of faunal affinity between the various basins; tabulated these affinities in terms of orders of similarity; and constructed an elaborate matrix to display them numerically. Yet only incidentally in the midst of all this '*Tabellenstatistik*' (as its critics scornfully called it) did Bronn record the fractional proportions of extant species in the various basins. Only these figures—a minor feature of one of his seventeen separate tables (Bronn 1831, table 11)—are conceptually equivalent to the percentages that Lyell was to use in his later analysis of the Tertiary. Bronn did use the proportion of extant species to indicate that the strata near Turin were quite separate from the Subappenine strata (as Lyell had also concluded); but he did not develop this into a general criterion of geological age, and his published work shows no theoretical structure underlying his 'statistical' analysis. Like some more recent palaeontologists who have been keen to exploit statistics in the modern sense of the word, Bronn gives the impression of having had more figures than he knew how to handle, and of not having had any clear theory that he wished to test.

THE ARTICULATION OF LYELL'S FAUNAL CHRONOMETER

Lyell described his period of collaborative work with Deshayes in 1829 in the following terms: 'We planned together a grand scheme of cataloguing the tertiary shells of various European basins, that I might draw geological inferences therefrom.' The intended division of labour is here quite clear! Later in the same letter, Lyell made equally clear the ambitious scope of his project: 'My results will be an induction from nearly (perhaps more than) 3000 species in the tertiary formations alone, and I hope by other aid than Deshayes to carry it on through older strata also' (Mantell MSS., Lyell to Mantell, 24 Feb. 1829). In other words, Lyell hoped that quantitative faunal comparison—a 'statistical' palaeontology—would yield a *general* faunal chronometer for the whole of the fossil record, not just the Tertiary. Given Lyell's concept of successive turnovers or 'revolutions' in the specific composition of, say, the molluscan fauna, there was no reason in principle why the chronometer should be limited to the most recent complete cycle of organic change. If some earlier 'moment' of geological time were taken as the base-line for comparison, in place of the present, it would be possible to estimate the ages of still older strata by their degree of faunal approximation to that base-line. In this way the chronometer could in principle be extended backwards indefinitely through one faunal cycle after another. Such an ambitious scheme was never again explicitly stated by Lyell, except very briefly and much later (Burchfield 1975, p. 68). Yet my analysis of his intention is consistent with what Lyell did make explicit, and I believe it represents the full scope of Lyell's original 'dream' of what his faunal chronometer might achieve.

Lyell had to make this grandiose project concrete in the first instance, however, by dating the Tertiary strata alone. During a period of intensive work after his return to

England, hints in his letters reveal how far his conception of the Tertiary stratigraphical record differed from that of Deshayes and Desnoyers. For example, he told Murchison: 'My last tour persuaded me that altho' on enlarging our Geology in new countries the epochs will multiply, yet in any one country the groups [of strata] will be found to belong to much fewer geological epochs than our predecessors imagined' (Murchison MSS., Lyell to Murchison, 5 Oct. 1829). Here the word 'epoch', like the words 'statistics' and 'revolution', needs careful interpretation. In the early nineteenth century the older sense of 'epoch', meaning a *point* or moment in time, still co-existed alongside the secondary (and modern) meaning of a *period* of time. Lyell's use of the word in the passage just quoted was in a sense a blend of the two meanings. Of course he did not think that any group of strata had been deposited in a 'moment' of time, even in geological terms: on the contrary, he was centrally concerned to emphasize how slowly all sediments have accumulated. Yet the quotation does imply that he envisaged that the time taken for the deposition of any one formation was quite short in comparison with the totality of time represented by all the formations of the same general age in different regions. To put it another way, Deshayes and Desnoyers hoped that by faunal and stratigraphical comparison the Tertiary formations of different regions could eventually be linked together in an overlapping 'chain' that would provide a *continuous* record of sedimentation and marine life. Lyell, in contrast, believed that these formations represented mere isolated 'moments' (relatively speaking), separated from each other by vast spans of geological time of which no record had been preserved; and even future exploration would merely multiply the number of these 'moments' of preserved time without ever achieving a continuous record.

Lyell returned to Paris in 1830 to work with Deshayes again, but the publication of his interpretation of Tertiary earth-history was delayed by the unexpected magnitude of his task of describing and classifying the agents of change at present observable in the inorganic and organic realms. This work was published in the first two volumes of the *Principles of geology*, and only in 1833 did Lyell finally publish the last volume, in which the Tertiary was used as an 'exemplar' of his method of interpretation of the past 'by reference to causes now in operation'.

In his exposition of his new system for the Tertiary, Lyell used once more the Brocchian analogy between species and individuals, and wrote quite casually about the 'birth and death of species' (Lyell 1833, pp. 32, 33). He explained his theory that the extinction of species is a normal part of nature, and that it happens in a piecemeal manner at all times. In the previous volume he had in fact rejected Brocchi's 'old age' explanation of extinction and replaced it with a more 'modern' theory based on environmental change (Lyell 1832, pp. 128–130). But this scarcely reduced the value of Brocchi's general analogy, and Lyell used it with great effect in his exposition, adapting it into a *human* analogy based on the contemporary concern with population censuses (Lyell 1833, pp. 31–33; Rudwick 1977). Lyell likened the continual shifts in the areas of sedimentation (and hence of the possibility of preservation of the fauna) to the movements of itinerant 'commissioners' taking censuses of the population in different regions of a country. Each preserved fauna in a given Tertiary basin was thus like the 'statistical documents' that such officials might leave behind them, to record the state of the population in a given province at a certain time. On their next visit, the constituent individuals in the population would have changed, by deaths and births, in proportion to the time since the previous census. Likewise the change in the fauna between two successive formations would also be proportional to the unrecorded interval of time between them.

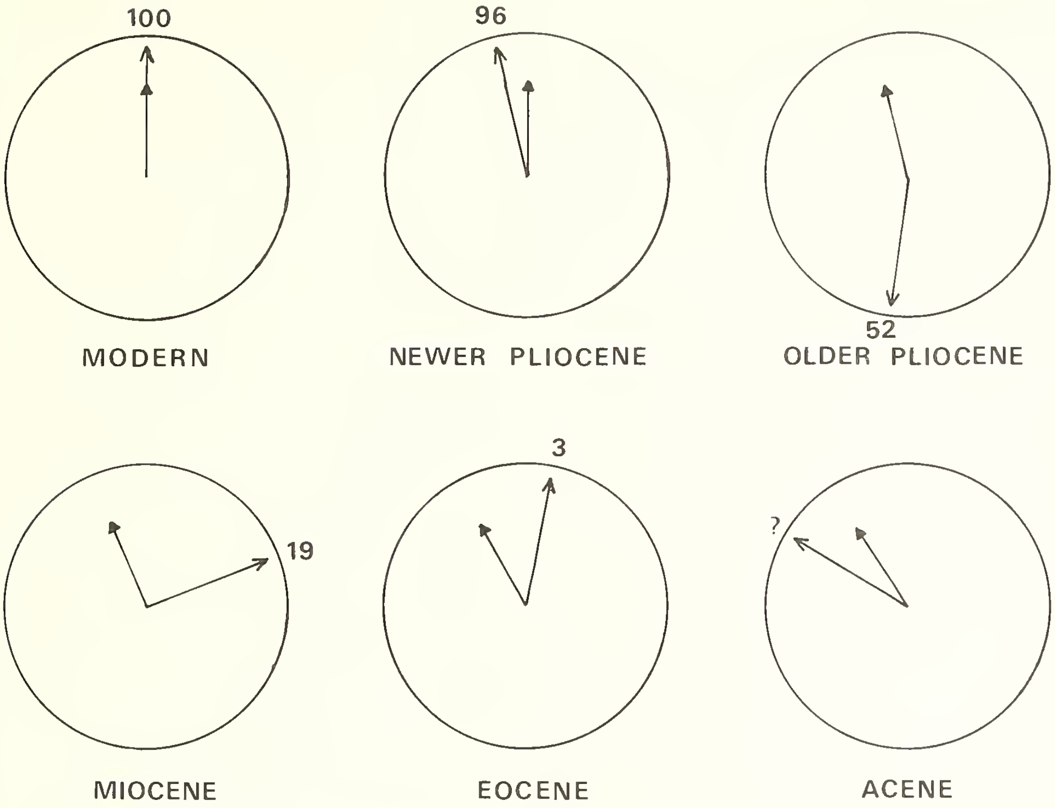
Obviously the analogy—like all analogies—had its limitations. Lyell was not postulating that the regularity of censuses had any analogue in the highly irregular fluctuations in the areas of Tertiary sedimentation. Conversely, he did want to use a quantitative comparison of faunas as a measure of time-differences not only between formations in one basin, but between formations in different basins. Nevertheless, the analogy was a helpful expository device for Lyell's readers, and it may also have been an important heuristic device at an earlier stage in Lyell's own mind. In any case, the population analogy served to make clear Lyell's distinctive concept of the various Tertiary formations as little more than momentary *samples* preserved from a vastly greater span of unrecorded time.

Lyell's introduction (1833, pp. 52–56) of the terms Eocene, Miocene, and Pliocene must be seen in the light of this conception of an extremely fragmentary geological record. Like other British scientists of this period, Lyell had applied to the polymathic William Whewell (1794–1866) for advice on his scientific nomenclature. Their letters reveal the barbarous Greek-based terms that might have entered the geologist's vocabulary—for example, 'Meiosynchronous', 'Meioneous', and 'Meiotautic'—before Whewell as an afterthought suggested 'Miocene', and of course 'Eocene' and 'Pliocene' too (quoted in Wilson 1972, pp. 305–307). Lyell also originally wanted an earliest 'Asynchronous' epoch, which in Whewell's hands became 'Acene'. Although the Acene was dropped from Lyell's published scheme, it is important for reconstructing his conception of the Tertiary epochs.

In earlier brief analyses of Lyell's work on the Tertiary, I interpreted Lyell's application of Deshayes's quantitative data in terms of a quite sophisticated conception of statistical survivorship rates (Rudwick 1970, pp. 24–26; 1972, fig. 4.5). This now seems likely to be anachronistic, since such statistics, in a form that Lyell might have recognized as relevant to his concerns, were not developed until the 1840s by the pioneer Belgian statistician Adolphe Quetelet (1796–1874). Lyell probably had a much simpler conception of the continual turnover of species during geological time, by which the percentage of extinct species in a Tertiary fauna would be directly proportional to its age.

It is probably consistent with Lyell's conception to depict his successive epochs in terms of a chronometer with a decimalized 'minute' hand (text-fig. 1). Suppose then that each 'hour' represents one complete faunal cycle or Lyellian 'revolution'. If the present (Lyell's 'modern' period) is represented by twelve noon, we can infer that Lyell conceived Deshayes's original estimates as follows: Deshayes most recent strata, which Lyell termed 'Newer Pliocene' (and later, 'Pleistocene'), were only 4% of the last 'hour' before 'noon'; his third epoch, Lyell's 'Older Pliocene', was just after the half-hour (52%); his second epoch, Lyell's 'Miocene', was only 19% through that last 'hour'; and his first epoch, Lyell's 'Eocene', was only 3% after 'eleven o'clock'. The provisional 'Acene' would then have represented some time *before* 'eleven o'clock', i.e. during the previous 'revolution', for it contained *no* extant species.

This analogy with a chronometer does not imply that Lyell thought that each of



TEXT-FIG. 1. Diagrammatic interpretation of Lyell's original conception of the 'epochs' of Tertiary time, in terms of a faunal 'chronometer'.

Deshayes's epochs represented no more than 1% of the total duration of a 'revolution'; he was certainly aware that Deshayes's figures could not claim any such accuracy. Further collecting was continually enlarging the fauna known from each formation, and the figures that Deshayes finally submitted to Lyell for publication in the *Principles* differed slightly from his earlier estimates: Eocene 3¼%, Miocene 18%, and (Older) Pliocene 49% (Lyell 1833, Appendix I, pp. 47–52). Yet even if Lyell realized the margin of error intrinsic to Deshayes's estimates, the suggested analogy with a chronometer does serve to emphasize that he did not think of his four periods (Deshayes's three, plus the Newer Pliocene) as periods that collectively recorded most of Tertiary time. He did, indeed, believe that the Newer Pliocene graded insensibly into the present. This was essential to his aim of breaking down the conceptual barrier between present and past, just as in Deshayes's view it disqualified the Newer Pliocene from being a real separate epoch. But between his four periods Lyell certainly believed that there were long spans of unrecorded time. He stated explicitly that the definition of these four periods was essentially a result of the accidents of preservation and collection, so that the periods were in a sense arbitrary; and he anticipated that intermediate periods would need to be defined in future (Lyell 1833, pp. 56–58). This makes it clear once more that to Lyell the known Tertiary faunas were no more than scattered samples from a far longer time-span of continuous change; they were *not*, as they were for Deshayes, a relatively complete record of a sequence of faunally distinct periods.

Lyell was always prudently cautious in public about suggesting any estimate in *years* for the magnitude of the geological time scale. Such reticence was prudent, not because Lyell had any reason to fear persecution or even ridicule by religious conservatives, but he knew that no estimate could be more than an enlightened guess, and that any such guess would be criticized by other geologists as a mere speculation running counter to the spirit of empirical science (the reception of Darwin's later rash guess is instructive: see Burchfield 1974).

In the *Principles*, the nearest that Lyell came to any calibration of geological processes in relation to human history was in his analysis of the volcano Etna. Here he estimated some 12 000 years for the accumulation of a small (unspecified) fraction of the volcanic cone, all of which post-dated the most recent Newer Pliocene strata of Sicily (Lyell 1833, pp. 97–101; Rudwick 1969). Privately, Lyell extended this estimate slightly in a way that hints at the kind of calibration that he envisaged for his faunal chronometer. In a letter to his sister, written while working in Paris with Deshayes in 1830, Lyell reported: 'This morning all my Etna shells were examined; out of sixty-three, only three species are not known to inhabit the Mediterranean; yet the whole volcano nearly is subsequent to them and rests on them. They lived on a moderate computation 100 000 years ago and after so many generations are unchanged in form' (K. Lyell 1881, p. 308). This and similar unpublished comments (see Tasch 1977) suggest that Lyell was estimating a period of the order of a million years for one complete faunal cycle or 'revolution', such as was represented by the whole of the Tertiary. This order of magnitude may seem unimpressive by modern standards, but it records a significant phase in the gradual stretching of the scientific imagination that enabled ever longer estimates to seem to geologists first conceivable, then plausible, and finally inescapable.

CONCLUSION

The first edition of Lyell's *Principles of geology* thus introduced the terms Eocene, Miocene, and Pliocene in a form that superficially resembles other stratigraphical terms of the nineteenth century. On the surface they seem to denote a sequence of contiguous periods of geological time, each with a distinct fauna. It might seem that the only difference between these Tertiary terms and the terms introduced for other parts of the stratigraphical record was that the Tertiary strata generally lacked easily identifiable 'characteristic fossils', so that they had to be distinguished by reference to the over-all character of the whole faunal assemblage. This was, roughly speaking, Deshayes's conception of the Eocene, Miocene, and Pliocene; and the later history of the terms shows that most other palaeontologists and geologists interpreted Lyell's terms in this way.

I have tried to show, however, that such an interpretation profoundly mistakes Lyell's own original intentions. In his early letters and notebooks, and even in his explanation of his terms in the first edition of the *Principles*, it is possible to detect a quite different and profoundly innovative conception. Lyell interpreted the Tertiary earth-history of Europe in terms of a continual flux of the physical and biotic environment, in which areas of sedimentation—and hence areas of preservation of the fauna and flora—had shifted irregularly in an almost aleatory manner. All the while the composition of the fauna and flora had been changing continuously but gradually, by the piecemeal introduction of new species (by *means* that remained obscure) and the equally piecemeal extinction of old ones. From this extremely complex network of interrelated inorganic and organic change, the fossil record hitherto examined had, as it were, 'caught on the wing' a few spatially scattered samples from four temporally isolated epochs. These were the Eocene, Miocene, Older Pliocene, and Newer Pliocene. Further collecting would doubtless add new samples, but the record could not be expected ever to approach completion. But such new samples could be fitted into a quantitative framework of geological time already provided in outline by the known Tertiary molluscan faunas: the slow but broadly uniform rate of faunal change provided a chronometer for the whole of Tertiary time, which constituted the last faunal cycle or 'revolution' in organic life.

Lyell's dream of a 'statistical' palaeontology that could provide a quantitative chronology for geology faded very quickly. The complete faunal discontinuity between the oldest Tertiary (Eocene) and the youngest 'Secondary' strata (Maastricht) perhaps discouraged him from even attempting to carry out his original project of extending his 'chronometer' backwards in time beyond the last faunal cycle. Even for the Tertiary faunas, his quantitative method found little understanding and much criticism from his contemporaries; and Lyell gradually diluted his original conception of the Tertiary epochs, stressing 'the per-centage test' of age less and less, until the epochs became almost indistinguishable from other more conventional stratigraphical units (e.g. Lyell 1838, pp. 286–289).

This fading of Lyell's original 'dream' cannot be traced here, but one major reason for it can be summarized briefly. The percentage test depended on the strict comparability of the specific units on which it was based. Although Lyell, like almost all other naturalists, believed in the ultimate reality of species, the distinction between taxonomic 'splitters' and 'lumpers' was already well known. Lyell therefore emphasized that the value of his percentage figures depended on the fact that they were based on identifications made by one single palaeontologist, Deshayes, who could be presumed to have used the same criteria of specific limits throughout (Lyell 1833, p. 51). Problems arose, however, as soon as other palaeontologists of a more 'splitting' disposition started calculating the percentage of extant molluscan species in the same Tertiary faunas (see Wilson 1972, chapter 14).

Lyell's quantitative analysis of the Tertiary molluscan faunas therefore failed as a result of the empirical difficulty of defining the limits of intra- and inter-specific variation. It failed at precisely the same period—the later 1830s—when Lyell's younger friend Charles Darwin (1809–1882) was privately struggling with a theory of trans-specific change that converted the taxonomists' empirical difficulty into a theoretical answer (see e.g. Limoges 1970; Gruber 1974). Darwin's evolutionary theory was based precisely on pursuing the taxonomists' problem to its limits, questioning the assumption of Lyell (and others) that there must be *some* intrinsic limit to variation. Thus the failure of Lyell's project for a quantitative faunal chronometer, and the success of Darwin's project for explaining the origin of new species, were both parts of a much broader collective enterprise in which most naturalists in the 1820s and the 1830s were engaged.

Lyell's dream of a 'statistical' palaeontology is worth recalling because it records an important early attempt to construct a quantitative time-scale for the history of the earth, against which other events and processes, both inorganic and organic, could be plotted and measured. Although Lyell's attempt failed, his insistence on the vast span of geological time kept the problem alive. It was largely in response to his persistence that the project of constructing a geological 'chronometer' was taken up again in earnest in the second half of the nineteenth century, using a variety of mainly physical methods (Burchfield 1975). It was that tradition that led directly to the radiometric dating of the twentieth century, which has freed palaeontology from its subservience to stratigraphy and enabled it to 'come of age' as the temporal dimension of biological science.

Acknowledgement and note. I am greatly indebted to the Council of the Palaeontological Association for the invitation to give the Twentieth Annual Address. I have rewritten the lecture into a form more suitable for publication, while retaining the content essentially unchanged. At the specific request of some who heard the lecture, I have included fairly full cross-referencing to my other publications in this field, since most of them are in periodicals that will be less familiar to palaeontologists than they are to historians of science.

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FOSSILS FROM THE MIDDLE-UPPER CAMBRIAN TRANSITION IN THE NUNEATON DISTRICT

by A. W. A. RUSHTON

ABSTRACT. In Britain the Middle-Upper Cambrian transition is fossiliferous only in the Nuneaton district. The *Lejopyge laevigata* Zone (Middle Cambrian) is recognized by a sparse fauna, chiefly of agnostid trilobites of Scandinavian character. The *Agnostus pisiformis* Zone (Upper Cambrian) contains Scandinavian agnostids and bradoriid Crustacea and also agnostids known from North America and Siberia, and rare polymerid trilobites akin to forms from Asia, Australia, and the U.S.A. *Cristagnostus papilio* gen. et sp. nov. and *Modocia anglica* sp. nov. are described.

In the Cambrian successions in Scandinavia, which furnish a biostratigraphical standard for much of the Cambrian in Europe and eastern Canada, the boundary between the Middle Cambrian and Upper Cambrian is taken between the *Lejopyge laevigata* Zone and *Agnostus pisiformis* Zone. In Sweden Westergård (1944; 1946; 1947; 1953) adopted the following zones and listed the fossils, especially trilobites, from each:

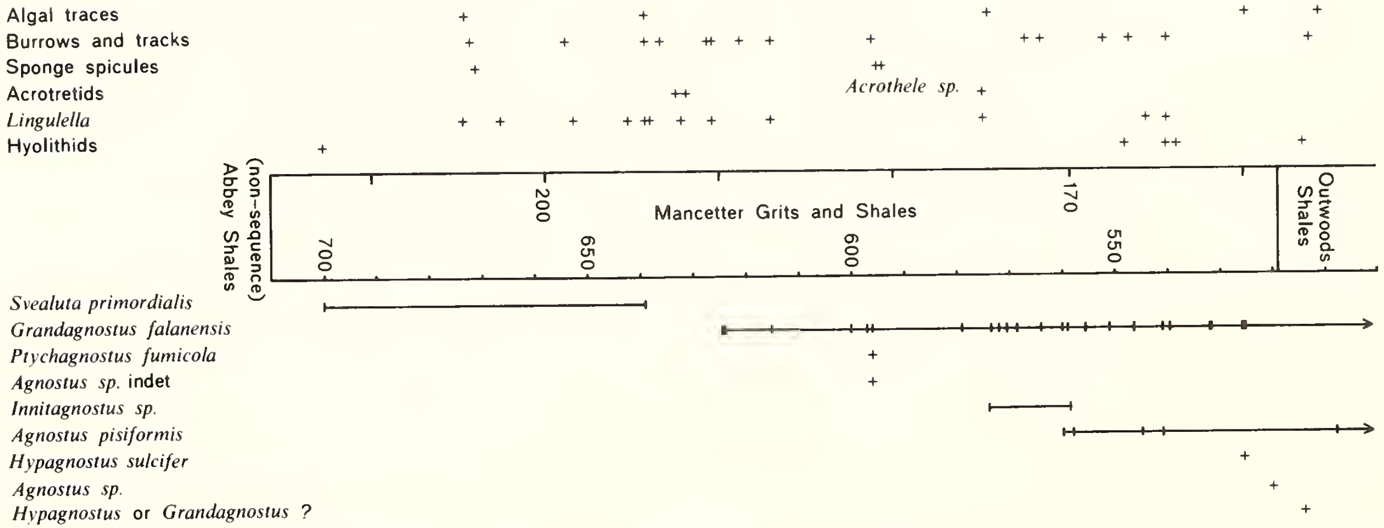
Upper Cambrian (lower part)	*Olenus* Zone (six subzones) *A. pisiformis* Zone
Middle Cambrian (upper part) = *Paradoxides forchhammeri* zonal group	*L. laevigata* Zone *Solenopleura brachymetopa* Zone *Ptychagnostus lundgreni–P.* (*Goniagnostus*) *nathorsti* Zone

Daily and Jago (1975) discussed the distribution of *L. laevigata* and the correlation of the Middle-Upper Cambrian boundary throughout the world.

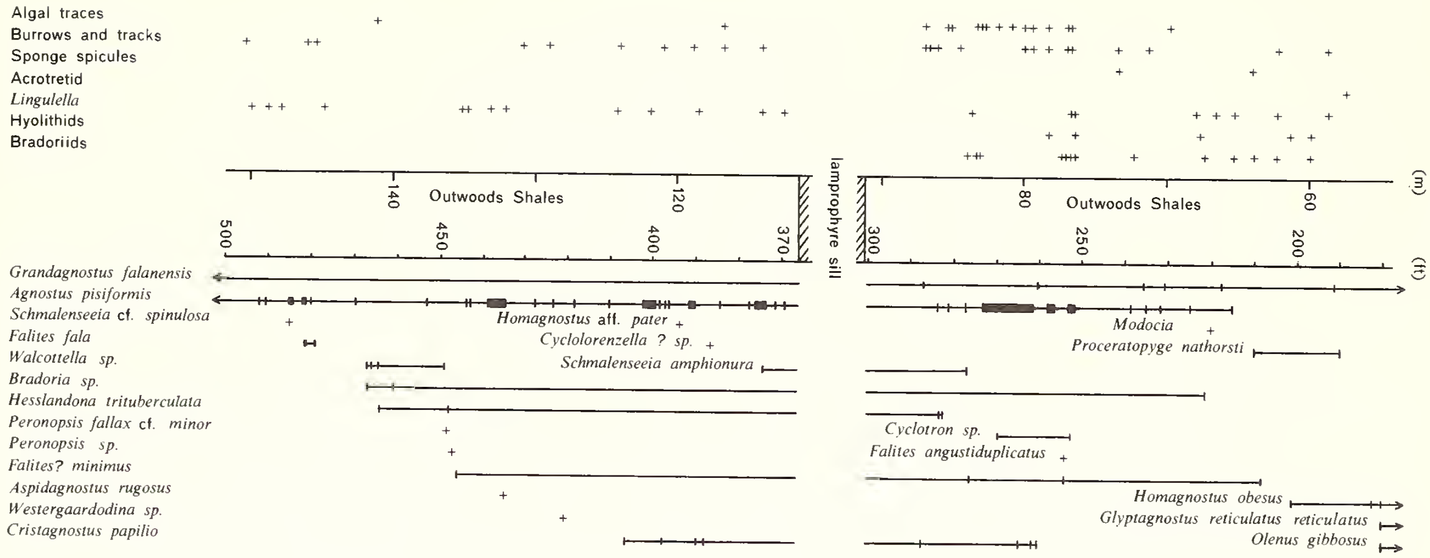
In most areas of Britain the Middle-Upper Cambrian boundary cannot be identified, the *A. pisiformis* Zone being unrecognized and the higher Middle Cambrian zones being only doubtfully represented (Taylor and Rushton 1972, pp. 9, 18). In the Nuneaton district, however, Taylor and Rushton showed that the *L. laevigata* Zone is present in the Mancetter Grits and Shales Formation and the *A. pisiformis* Zone is present in the lower 91 m of the conformably overlying Outwoods Shales Formation; they described the geology of these formations, deriving much of their information, and nearly all their fossils, from the Merevale No. 3 Borehole (op. cit., pp. 7, 10, 104; pl. 4).

Text-figs. 1 and 2 show the distribution of fossils in Merevale No. 3 Borehole, with species on the right of each column and the occurrence of undifferentiated taxa on the left.

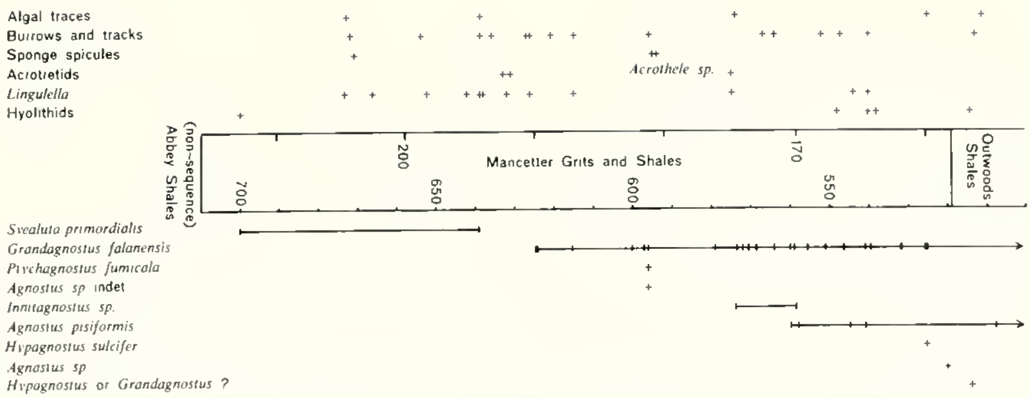
[Palaeontology, Vol. 21, Part 2, 1978, pp. 245-283, pls. 24-26.]



TEXT-FIG. 1. Distribution of fossils in the *Lejopyge laevigata* Zone in Merevale No. 3 Borehole. Occurrence of undifferentiated taxa on the left, ranges of species on the right.



TEXT-FIG. 2. Distribution of fossils in the *Agnostus pisiformis* Zone in Merevale No. 3 Borehole. Occurrence of undifferentiated taxa on the left, ranges of species on the right. *Proceratopyge nathorsti* and *Modocia* [= *M. anglica*] were collected at Purley Quarry; their stratigraphical position is plotted on the assumption that the incoming of *Olenus gibbosus* and *Glyptagnostus reticulatus* is at the same level in the Quarry as in the Borehole.



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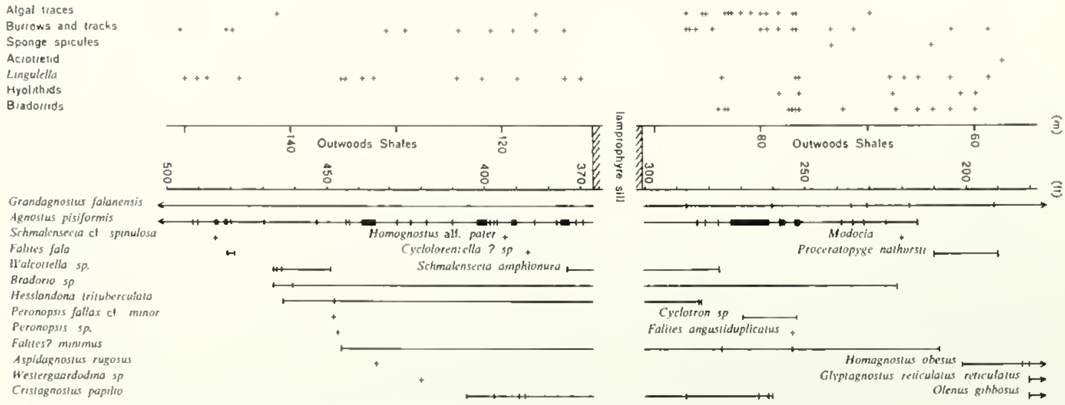

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CORRELATION OF THE FAUNAS

Lejopyge laevigata Zone

Westergård (1946; 1953) listed up to twelve species of polymerid trilobites and about twenty of agnostids from the *laevigata* Zone in Sweden, whereas the borehole yielded no polymerids and only eight species of agnostids (text-fig. 1*a*). Most of the forms present in the borehole are comparable with Swedish species, though the commonest form, *Grandagnostus falanensis*, is not recorded from the *laevigata* Zone in Sweden and the *Innitagnostus* species present resembles the Swedish *I. neglectus* (Westergård) less than it does some other species of the genus. However, *Ptychagnostus* (*Goniagnostus*) *fumicola* is known elsewhere only from Australia where it ranges from the '*laevigata* III' Zone to the *torosa-janitrix* Zone which Öpik (1967, p. 91) regarded as a Middle–Upper Cambrian passage zone. Daily and Jago (1975) have argued that this passage zone lies within the European *laevigata* Zone and below the Middle–Upper Cambrian boundary. Incidentally, a consequence of this revision of the correlation is to restore Öpik's 'Upper Cambrian' species of *Hypagnostus*, *Grandagnostus*, *Lejopyge*, *Ptychagnostus* (*Goniagnostus*), and *Olenoides* to the Middle Cambrian.

In Merevale No. 3 Borehole the *laevigata* Zone is estimated to be 55 m thick. The base is taken down to the base of the Mancetter Formation because *Svealuta primordialis* occurs almost at the base of the formation. Daily and Jago (1975, p. 540) suggested that the *brachymetopa* Zone might be indicated in the borehole but as I can find no confirmation that *S. primordialis* occurs below the *laevigata* Zone, I retain here the correlation originally proposed by Taylor and Rushton (1972, p. 8).

The erosional break between the Mancetter Grits and Shales and the underlying Abbey Shales indicates a regression at about the horizon of the *brachymetopa* Zone which in Sweden corresponds to the Andrarum Limestone and the Exporrecta Conglomerate (Martinsson 1974, p. 250). Furthermore, the *laevigata* Zone represents a transgression and marks the start of a new cycle of sedimentation in various areas of Sweden (summarized by Martinsson 1974), Newfoundland (Poulsen and Anderson 1975, discussed below), and Britain (Taylor and Rushton 1972, p. 9); it may be noted that poorly preserved agnostids indicative of the Middle Cambrian have been collected from near the base of the Maentwrog Beds (lower '*Lingula* Flags') in the Harlech Dome, North Wales (Rushton 1976, p. 115), thus showing that the '*Lingula* Flags' cycle of sedimentation commenced before the beginning of the Upper Cambrian in North Wales.

A comparable break occurs in Newfoundland. At localities in Manuels River and on Random Island, Poulsen and Anderson (1975) reported a lithological change between beds of the Manuels River Formation with a *Paradoxides davidis* fauna and the base of the overlying Elliott Cove Formation (or Group). They found fossils of the *laevigata* Zone within the basal 4 m of the Elliott Cove Formation at Random Island and the basal 1·5 m at Manuels River. In those places the *brachymetopa* Zone is absent; but half-way between them, at Highland Cove, Hutchinson (1962) found a '*Paradoxides forchhammeri* Zone' fauna which Poulsen and Anderson (1975, p. 2068) referred to the lower part of the *brachymetopa* Zone. However, there is insufficient palaeontological evidence to support this correlation, as Poulsen and Anderson (p. 2068) suggest: e.g. Hutchinson's '*Peronopsis* cf. *quadrata*' has a pygidial collar (1962, pl. 5, figs. 6, 7) and thus differs from the Swedish *P. quadrata* (Tullberg) from the *brachymetopa* Zone; furthermore, Hutchinson's fauna includes *Ptychagnostus hybridus* (Brögger) and *Pt. punctuosus* (Angelin), both of which are indicative of lower zones. Therefore the *brachymetopa* Zone is not yet proved in Newfoundland and may be altogether absent.

Hutchinson (1962, p. 27) recognized the *pisiformis* Zone above the base of the Elliott Cove Formation at Random Island, Manuels River, and Trinity Bay, but he thought that beds representing the *laevigata* Zone were absent or unfossiliferous in Newfoundland (1962, pp. 24, 27). However, three of his specimens of *Oidalagnostus* cf. *trispinifer* Westergård (Hutchinson 1962, pl. 7, figs. 17–19), though poorly preserved, seem identical to Westergård's species and thus indicate the *laevigata* Zone: they came from 16·5 m above the base of the Elliott Cove Formation in the Manuels River section. Hutchinson's fourth specimen of *O.* cf. *trispinifer* (1962, pl. 7, fig. 20), which evidently led him not to identify his material with *O. trispinifer* (s.s.), came from the same locality but from a higher level, 21·0 m above the base of the Formation; it is referable to *Cristagnostus papilio* sp. nov. and if it represents the *pisiformis* Zone, as in England, the base of the *pisiformis* Zone in the Manuels River section lies between 16·5 m and 21·0 m above the base of the Elliott Cove Formation. At Manuels River both *A. pisiformis* and *Grandagnostus* '*bairdi*' (= *falanensis*) range above and below these occurrences.

Agnostus pisiformis Zone

The fauna of the *pisiformis* Zone is more varied and cosmopolitan in character at Nuneaton than in Sweden where the facies was very favourable to *Agnostus pisiformis* but almost excluded other trilobites. The different environments indicated by the various mudstones of the Outwoods Shales seem to have allowed a wider variety of forms to make a sporadic appearance in the Nuneaton area. Of the species found there (text-fig. 2), some of the bradoriids and four of the trilobite species (*A. pisiformis*, *G. falanensis*, *Schmalenseeia amphionura*, and *Proceratopyge nathorsti*) occur in the *pisiformis* Zone in Sweden.

The *pisiformis* Zone is estimated to be 58 m thick in Merevale No. 3 Borehole. The base of the zone is taken at a depth of 485 ft 0 in. (147·83 m) where *Schmalenseeia* cf. *spinulosa* occurs with several specimens of *A. pisiformis* and a juvenile *Aedotes*? *S. spinulosa* was described from the *pisiformis* Zone in northern Siberia and is the lowest fossil in the borehole which can be taken to indicate the *pisiformis* Zone.

Of the other species present, *C. papilio* is known from the presumed *pisiformis* Zone at Manuels River in Newfoundland, as mentioned above. *Homagnostus* aff. *pater* is known (as '*Proagnostus bulbus*') at Cedar Bluff, Alabama, U.S.A., from beds assigned by Resser (1938, p. 33) to the *Cedaria* Zone, which was considered by Daily and Jago (1975, p. 542) to span the *laevigata–pisiformis* zonal boundary. *Aspidagnostus rugosus* occurs at Cedar Bluff, and also in Nevada, in beds overlying those with *Glyptagnostus stolidotus* Öpik and which therefore lie near or at the top of the *pisiformis* Zone. *A. rugosus* occurs at about the same horizon in northern Siberia (Datsenko *et al.* 1968, atlas, pp. 38, 39) and in the Altay Mountains (Poletaeva and Romanenko 1970, p. 72). *Modocia anglica* is referred to a genus known from several strata around the Middle–Upper Cambrian boundary in North America. *Cyclolorenzella* sp. is likewise referred to a genus known from around the Middle–Upper Cambrian boundary in China and especially from the Kushan Formation which Daily and Jago (1975, p. 543) considered to span this boundary.

The base of the overlying *Olenus* Zone is taken at 200 ft 8 in. (61·16 m) in Merevale No. 3 Borehole where the lowest specimen of *H. obesus* (Belt) occurs; another specimen was found at 189 ft 8 in. (57·81 m) and several at 182 ft 0 in. (55·47 m), just below the lowest *G. reticulatus* (Angelin) and *O. gibbosus* (Wahlenberg) at 180 ft 4 in. (54·96 m).

PALAEOENVIRONMENT

The Mancetter and Outwoods formations are thought to have been deposited in quiet offshore conditions of no great depth. They consist mainly of pale-grey to dark-grey laminated and unlaminated mudstones. Some of the pale beds are much burrowed (Taylor and Rushton 1972, pp. 7, 10), and these beds contain no body fossils apart from occasional inarticulate brachiopods (Pl. 26, figs. 18, 19), and never contain traces of algae. They represent comparatively well-aerated bottom conditions.

Some of the trilobites were found in dark unlaminated mudstones: most of these are represented by isolated specimens, many of which appear to represent exuvia (Henningsmoen 1975), e.g. *Grandagnostus falanensis*, *Cristagnostus papilio*, *Cyclolorenzella* sp., and *Modocia anglica*. Hyolithids occur sporadically in this type of mudstone (Pl. 26, figs. 16, 17). The dark laminated mudstones include horizons with abundant algal traces (Taylor and Rushton 1972, pl. 6, figs. 1, 2) and a general absence of bioturbation. These represent phases with little detrital sedimentation; the bottom conditions were deoxygenated and therefore unsuitable for grazing or burrowing benthos. The layers with algae sometimes also have crowds of *Agnostus pisiformis* (at higher levels *H. obesus* and *Olenus* spp. occur in this facies), together with small bradoriids (mainly juveniles), rare *Schmalenseeia*, and *Protospongia*-like sponges. Of these forms, the agnostids and *Schmalenseeia* may have been pelagic (Robison 1972; Jago 1972, p. 233) and therefore not affected by the bottom conditions; Henningsmoen (1957, pp. 79–82) and Fortey (1975) postulated that olenids were adapted to living in poorly oxygenated conditions. The mode of life of the bradoriids and sponges is not known, but *Protospongia* is found articulated in low-energy environments (including graptolitic facies) of Middle Cambrian to Arenig age, and it seems likely that it was adapted to such environments.

Palmer (1972) showed that, in the Cambrian, north-west Europe formed part of the 'shelf-margin—open ocean' palaeogeographic region and probably lay at high latitudes. Elements of the faunas of this region are comparatively widespread and are thought to have inhabited cool water, shallow at the poles but deeper in low latitudes (cf. Cook and Taylor 1975). Occasional agnostids from the Nuneaton district which were not previously recorded from Europe but were known from near the edge of the 'restricted shelf' regions (Palmer 1972) of the U.S.A., Siberia, and Australia probably migrated along belts of cooler water. The present research adds some polymerids exotic to Europe to the Swedish record of *Drepanura eremita* Westergård (1947)—*Aedotes*?, *Cyclolorenzella*, *Modocia*: these are related to forms from 'restricted shelf' regions (Palmer 1972) but were able to penetrate the barrier (of cold water according to Cook and Taylor 1975) which prevented most of the shelf region trilobites from migrating more widely.

SYSTEMATIC DESCRIPTIONS

The terminology for trilobites is generally that of Moore (1959). 'Glabella' refers to the pre-occipital part of the cephalic axis. The classification generally follows that of Moore (1959) except where superseded by Öpik (1967), whose treatment of Agnostida is followed here.

AGNOSTID TRILOBITES

Family AGNOSTIDAE McCoy, 1849

Subfamily QUADRAGNOSTINAE Howell, 1937

Peronopsis Hawle and Corda, 1847

Peronopsis fallax (Linnarsson, 1869) *minor* (Brögger, 1878)

Plate 24, fig. 1

1878 *Agnostus fallax* Linnarsson var. 3 *minor*; Brögger, p. 65, table opposite p. 34.
1946 *Peronopsis fallax minor* (Brögger, 1878); Westergård, p. 38, pl. 3, figs. 3–7.
1972 *Peronopsis* sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].
1976 *Peronopsis fallax* cf. *minor* (Brögger, 1878); Fortey and Rushton, p. 327, pl. 12, fig. 15.

Material. Internal mould of one specimen 6·0 mm long, BDA 1781.

Remarks. The cephalon agrees with the specimen in Westergård's plate 3, fig. 4, except that the anterior glabellar lobe is a little longer; the posterior glabellar lobe has a node slightly in front of its mid-length instead of at its mid-point; and there appears to be a very faint depression in front of the glabella, though in the specimen this is slightly emphasized by damage during preparation. It is doubtful if these slight differences are significant. The anterior glabellar lobe is longer and the basal lobes shorter than in the early Upper Cambrian form from Iran described by Fortey and Rushton (1976, pl. 12, figs. 1–14) as *P. fallax* aff. *minor*.

The pygidium of *P. f. minor* is variable. The rounded posterior to the axis of the present specimen resembles Westergård's fig. 6 but the axis reaches nearly, though not quite, to the marginal furrow, as in his fig. 7. The present specimen differs from all Westergård's figured specimens because the lateral edges of the pygidium do not diverge towards the posterolateral spines, but this may be due to compaction of the mudstone matrix of the Nuneaton specimen. *P.* [*Homagnostus*] *incerta* (Robison, 1964, p. 531, pl. 82, figs. 16, 17, 19, 20) has a wider glabella and a shorter, wider anterior glabellar lobe than the present specimen; the pygidial axis is fully half the width of the pygidium (less than half in the present specimen), and reaches to the marginal furrow; the border is considerably wider and the marginal spines are larger.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 448 ft 6 in. (136·70 m). *P. f. minor* occurs in the *Solenopleura brachymetopa* Zone in Scandinavia.

Peronopsis sp.

Plate 24, fig. 2

1972 *Peronopsis*? sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. External mould of one specimen 12·2 mm long, BDA 1776.

Description. Cephalon as long as wide, weakly convex. Glabella with individual convexity, surrounded by shallow axial furrow, two-thirds as long as cephalon.

Anterior lobe rounded in front, half as long as posterior lobe, quarter the cephalic width. Posterior lobe widens backwards to one-third of the cephalic width, rounded behind. Small median node at anterior quarter of posterior glabellar lobe. Basal lobes small, triangular, not well preserved. Cheeks confluent anteriorly. Border furrow narrow, border narrower than one-tenth of the cephalic length.

Thoracic axis not effaced.

Pygidium as long as wide, weakly convex. Axial furrows obscure but anterior ends are just visible, more than half pygidial width apart, dying out about one-third of the pygidial length from the anterior margin. Very faint furrows marking off the anterior lobes of the pygidial axis extend inwards from the axial furrows at about one-fifth of the pygidial length from the front. Elongate median node at anterior one-third of pygidial length. Border furrow marking off flat border about as wide as one-eighth of the pygidial length, and about twice as wide as the cephalic border. No marginal spine seen. Surface smooth.

Remarks. The present specimen, though not sufficiently well preserved to serve as a monotype of a new species, is clearly distinct from described species of *Peronopsis* in having the axial furrows distinct on the cephalon but nearly effaced on the pygidium. In the main stock of effaced peronopsids—*Hypagnostus* and *Cotalagnostus*—the glabella is effaced anteriorly and the pygidial axis is clearly outlined. It is unusual for an agnostid to have the cephalon less effaced than the pygidium, though such a condition might be claimed for *Delagnostus dilemma* Öpik (1961, p. 88) which, however, differs from the present form because it has no distinct pygidial border and the glabella is not clearly outlined anteriorly.

The present species differs from species of *Peronopsella* Sdzuy, 1967 because the

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EXPLANATION OF PLATE 24

Except where stated otherwise the specimens are in the collection of the Institute of Geological Sciences, London, and are internal moulds. All were whitened with ammonium chloride. Specimens marked M3 are from Merevale No. 3 Borehole; localities of other specimens are given more fully. Photographs by Mr. J. Evans.

Fig. 1. *Peronopsis fallax minor* (Brögger). BDA 1781, × 6. M3, 448 ft 6 in. (136·70 m).

Fig. 2. *Peronopsis* sp. BDA 1776 latex cast, × 4. M3, 447 ft 5 in. (136·37 m).

Figs. 3, 4. *Hypagnostus sulcifer* (Wallerius), × 6. M3, 525 ft 3 in. (160·40 m). 3, GSM 103278. 4, fragment of pygidium showing axial lobes. GSM 103280, latex cast.

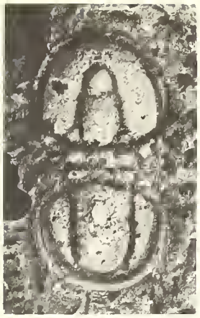
Fig. 5. *Hypagnostus* or *Grandagnostus*? sp. BDA 1967 latex, × 6. M3, 514 ft 4 in. (156·77 m).

Figs. 6–14. *Grandagnostus falanensis* (Westergård). 6, BDA 2257, × 6. M3, 624 ft 6 in. (190·35 m). 7–9, top, side, and back views of pygidium, holotype of *Phalacroma bairdi* Hutchinson (1962, pl. 11, fig. 9*b* only, not fig. 9*a*); 9 shows a valve of *Walcottella* in the foreground. Geological Survey of Canada 13055, × 6. Elliott Cove Formation, Manuels River, South-eastern Newfoundland. 10–12, holotype, side, back, and top views. Sveriges Geologiska Undersökning, figured Westergård 1947, pl. 1, fig. 14, × 7. *Agnostus pisiformis* Zone, Djupadalen, Västergötland, Sweden. 13, pygidium, BDA 2210, × 6. M3, 599 ft 8 in. (182·78 m). 14, juvenile form BDA 2205, × 12. M3, 597 ft 0 in. (181·97 m).

Figs. 15–19. *Agnostus pisiformis pisiformis* (Wahlenberg), M3. BDA 1632, 400 ft 7 in. (122·10 m); BDA 1699 latex, 427 ft 11 in. (130·43 m); BDA 1415, 271 ft 6 in. (82·75 m); BDA 1398 latex, 268 ft 4 in. (81·79 m); BDA 1417 latex, 271 ft 8 in. (82·80 m). All × 6.

Fig. 20. *Innitagnostus* sp. Flattened cephalon, BDA 2094, × 12. M3, 558 ft 6 in. (170·23 m).

Fig. 21. *Agnostus* sp. BDA 1984, × 6. M3, 520 ft 0 in. (158·50 m).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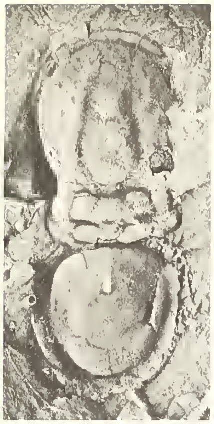
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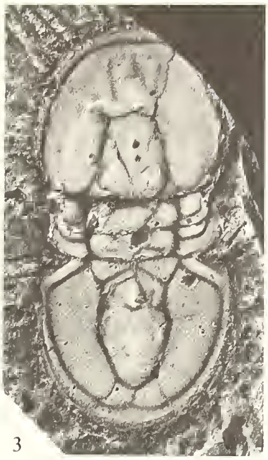
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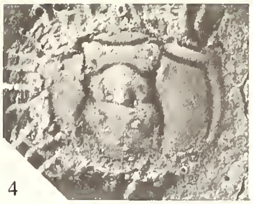
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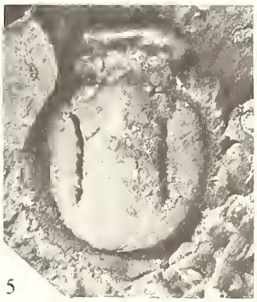
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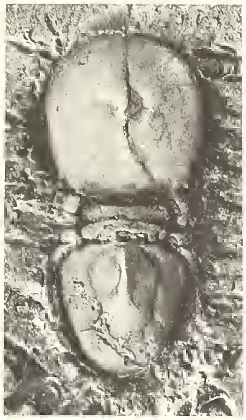
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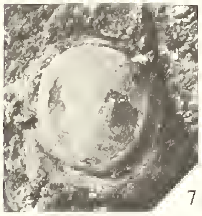
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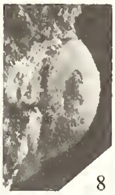
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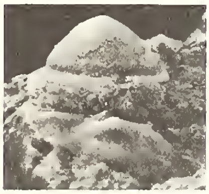
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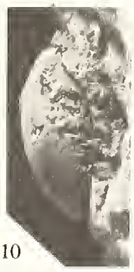
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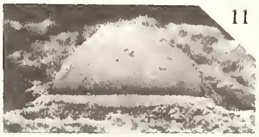
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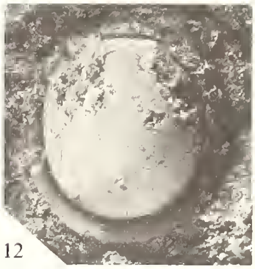
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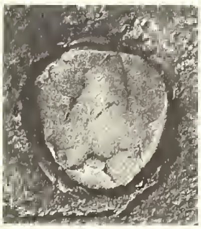
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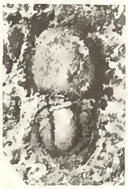
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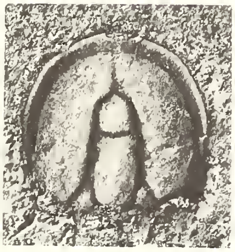
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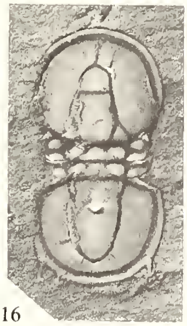
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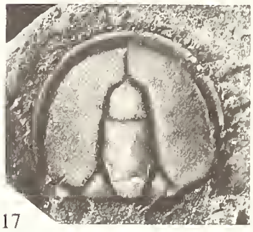
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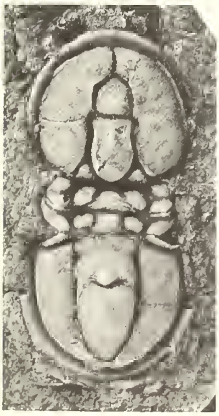
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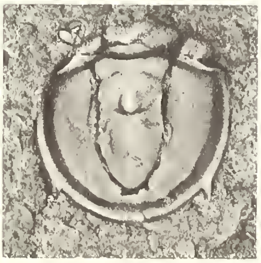
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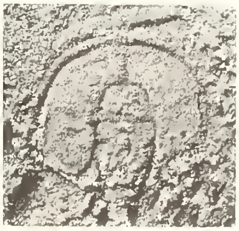
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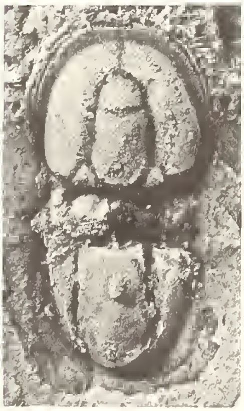
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RUSHTON, Cambrian trilobites

glabella is outlined all round. Two species in which the cephalon is imperfectly known, *P. spinata* (Illing) and *P. definita* (Howell), differ from the species described above because the pygidial margin bears a pair of comparatively large spines and the axial furrows are more distinct anteriorly. (It is improbable that the present form is related to *Peronopsella* which is based on a close-knit group of mid-Middle Cambrian species.)

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 447 ft 5 in. (136·37 m).

Hypagnostus Jaekel, 1909

Hypagnostus sulcifer (Wallerius, 1895)

Plate 24, figs. 3, 4

1895 *Agnostus exsculptus* Angelin forma *sulcifera* Wallerius, p. 38, pl. 1, fig. 1*a*, *b*.
1946 *Hypagnostus sulcifer* (Wallerius, 1895); Westergård, p. 52, pl. 6, figs. 7–17.
1972 *Hypagnostus sulcifer* (Wallerius); Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. Three complete specimens, 9·2 mm, 7·8 mm, and 4·8 mm long, and a fragmentary pygidium; GSM 103278–103282; all from a single slickensided layer in Merevale No. 3 Borehole.

Remarks. The cephalon of *H. sulcifer* differs from those of *H. exsculptus* (Angelin) and *H. scrobiculatus* Westergård because the glabella tapers slightly and is clearly limited anteriorly. The glabella of *H. sulcifer*, unlike the other species, has at most a very weak median node. The pygidial axis of *H. sulcifer* is more clearly divided by transverse furrows than that attributed to *H. exsculptus*. Öpik (1961, p. 60) has discussed the differences between *H. sulcifer* and *H. hippalus*; the latter has a quite different pygidium. *H. durus* Öpik, 1967 has a shorter, truncate glabella and its pygidium, though furrowed like that of *H. sulcifer*, differs in having marginal spines.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, at 525 ft 3 in. (160·40 m). In Sweden it occurs in the upper part of the same zone.

Hypagnostus (or *Grandagnostus*)? sp.

Plate 24, fig. 5

cf. 1946 '*Agnostus*' sp. No. 8; Westergård, p. 99, pl. 16, fig. 21.
1972 '*Ciceragnostus*'-like pygidium; Taylor and Rushton, p. 18.

Material. External mould of one pygidium with part of thorax, BDA 1967; the pygidium is 4·4 mm long.

Description. Pygidial length equal to width. Axis outlined for three-fifths of pygidial length, for the most part parallel-sided, less than half the maximum width, but expanding anteriorly to a little more than half the maximum width. Posteriorly the axial furrows become very faint, turn inwards but do not meet, nor do they reach the border furrow. Elongate median node at the anterior quarter. Border flat, broad (more than one-tenth of the length and breadth of the pygidium).

Remarks. This specimen resembles the pygidia described by Westergård (1946) as '*Ciceragnostus*' (as discussed below the Middle Cambrian forms related to *A. cicer* Tullberg may be referred to *Grandagnostus* but not *Ciceragnostus*). Although Taylor and Rushton compared the present specimen with Westergård's plate 16, fig. 6, it has a lower convexity and a wider border, and is nearer to '*Agnostus*' sp. No. 8 in his plate 16, fig. 21. It differs from that form because the axis widens somewhat towards the articulating half-ring and the axial furrows extend a little further back and tend to turn in towards the mid-line posteriorly. In these respects it agrees better with the pygidia illustrated by Westergård as '*Agnostus*' sp. No. 4 (1946, pl. 16, figs. 13–17), which Öpik (1961) suggested might belong to a *Hypagnostus* species; those forms, however, have a narrower axis than the present specimen. Without knowledge of the cephalon the generic reference remains uncertain.

A comparable pygidium occurs in equivalents of the *pisiformis* Zone at Cherry Creek and McGill, Nevada (Palmer 1962, pl. 1, figs. 32, 33), but in that form the width increases towards the articulating margin and the axial furrows are relatively shorter and further apart.

Occurrence. Merevale No. 3 Borehole, at depth 514 ft 4 in. (156·77 m), 1 m above the base of the Outwoods Formation as recognized in that borehole, *laevigata* Zone or possibly *pisiformis* Zone. The pygidium '*Agnostus*' sp. No. 8 of Westergård is from the *laevigata* Zone, upper part, in Sweden.

Grandagnostus Howell, 1935*a*

Remarks. The type species *G. vermontensis* Howell (1935*a*) is poorly known but the genus was framed with *A. glandiformis* Angelin (Westergård 1946, pl. 15, figs. 3–17; pl. 16, figs. 1, 2) also in mind (Howell 1935*a*, p. 221). Öpik (1961, p. 54) and Jago (1976, p. 144) have discussed the genus. *Grandagnostus*, as interpreted here, includes effaced agnostids with a broad border on the pygidium but none on the cephalon; they are probably peronopsids representing the end of the sequence *Peronopsis*–*Hypagnostus*–*Cotalagnostus*–*Grandagnostus*. Basal glabella lobes may be present or absent. The pygidial axis may be effaced or partly developed and is long, as shown by vestigial axial furrows or by the terminal axial node. Species referred to the genus include *A. bituberculatus* Angelin and *A. cicer* Tullberg (Westergård 1946), *Ciceragnostus*? *falanensis* Westergård, 1947, *Phoidagnostus angustiformis* Pokrovskaya, 1958, *Phalacroma maja* Pokrovskaya, 1958 [? *pars*], *G. velaevis* Öpik, 1961, *Phalacroma bairdi* Hutchinson, 1962, and *Grandagnostus* sp. of Jago (1976). Species with a cephalic border and broad pygidial border were grouped in *Valenagnostus* Jago, 1976 (p. 142), with *V. marginatus* (Brögger) as type species.

Öpik (1967, pp. 76, 82) showed that neither of the genera *Phalacroma* Hawle and Corda, 1847, nor *Phoidagnostus* Whitehouse, 1936, can be used for these agnostids. He also showed (1961, p. 53) that *A. cicer* should not be placed in *Ciceragnostus* Kobayashi, 1937. Juveniles of *G. falanensis* described below resemble *A. cicer* and also *Hypagnostus*, showing that they were descended from the peronopsid stock. Accordingly *Grandagnostus* is extended here to include forms in which part of the pygidial axis is distinctly outlined in full-grown specimens, as in *A. cicer*. *G. bituberculatus* has a pygidium typical of *Grandagnostus* but the cephalon has distinct basal glabellar lobes, the presence of which led Öpik (1961, p. 54) to refer it to *Phalagnostus* Howell, 1955 (type species *Battus nudus* Beyrich). In *Phalagnostus*, however, the axis is not effaced but is large and subcircular, and the 'border' is composed of the flanks with or without the border. Rasetti (1967, p. 38; also Jago 1976, p. 146) tentatively proposed this interpretation because the anterior border furrow, instead of delimiting the anterolateral border, crosses the border-like structure. Having examined Bohemian and British material of *Phalagnostus* I agree with Rasetti and consider that the ontogenetic development of the pygidium (Šnajdr 1958, p. 79) also confirms this interpretation. Other species of *Phalagnostus* include *A. eskriggei* Hicks, *A. nudus scanicus* Tullberg, *P. prantli* Šnajdr, *Phalacroma calvum* Pokrovskaya, and *A. n. ovalis* Illing; the last named is the type species of *Phalacromina* Kobayashi (1962, p. 29), which is therefore a junior subjective synonym of *Phalagnostus*. Some unnamed pygidia (Westergård 1946, pl. 16, fig. 3; Hutchinson 1962, pl. 12, fig. 1; Rasetti 1967, pl. 10, figs. 22–26) have a comparable structure but the corresponding cephala have not been recognized.

Peratagnostus Öpik (1967, p. 86) can be distinguished from *Grandagnostus* because the pygidial border is narrower, its width posteriorly being less than one-tenth of the length of the pygidium; the axis is narrow and ends well short of the posterior border in described species (Palmer 1968, p. 26).

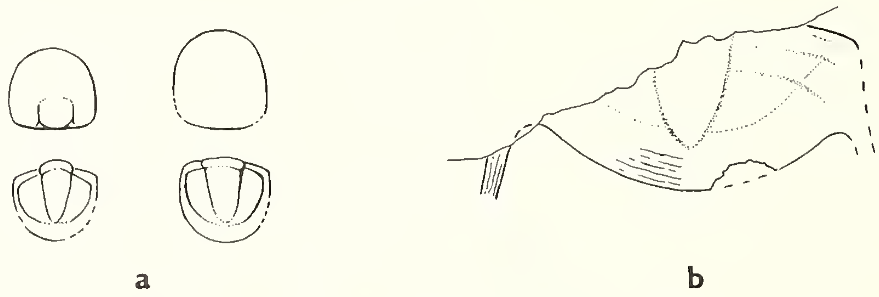
Grandagnostus falanensis (Westergård, 1947)

Plate 24, figs. 6–14; text-fig. 3*a*

1947 *Ciceragnostus*? *falanensis* n. sp.; Westergård, p. 7, pl. 1, fig. 14.
1962 *Phalacroma bairdi* n. sp.; Hutchinson, p. 90, pl. 11, figs. 9–11.
1972 *Grandagnostus bairdi* (Hutchinson); Taylor and Rushton, pp. 8, 18, 20, text-fig. 4 [recorded].
1975 *Lejopyge laevigata* (Dalman, 1828); Poulsen and Anderson [*pars*], p. 2076, pl. 2, figs. 1?, 4?, 7, 8.

Material. About forty specimens from the Mancetter Formation in Merevale No. 3 Borehole, including BDA 1986–1987, 1995–1997, 2004–2006, 2014–2015, 2017, 2019–2020, 2029–2033, 2038–2039, 2041–2042, 2051–2052, 2067–2068, 2097, 2106, 2124, 2137, 2139–2142, 2148–2149, 2172–2175, 2191–2195, 2197–2198, 2205–2210, 2242–2243, 2257–2266. A few specimens from the upper part of the *pisiformis* Zone in the Outwoods Formation in the borehole (e.g. BDA 1188, 1205–1206, 1222, 1314–1315) and several from a similar horizon at Purley Quarry (RU 2180–2209). Many specimens from the *Olenus* Zone. Most of the specimens are more or less flattened or crushed.

Description. Cephalon domed, usually a little longer than wide. A trace of the basal lobes and posterolateral borders seen in some specimens but no lateral or anterior



TEXT-FIG. 3. *a*, *Grandagnostus falanensis* (Westergård), two meraspides of degree 1, showing pygidial axis and part of glabella. Both on BDA 983, × 16. *Olenus* Zone, Merevale No. 3 Borehole, 168 ft 0 in. (51·21 m). *b*, *Proceratopyge nathorsti* Westergård. Fragmentary pygidium RU 122, × 8. Locality as for Plate 26, fig. 4.

border. Small node just behind mid-length of cephalon occasionally seen. Some internal moulds show a thin groove extending just within and roughly parallel to the lateral and frontal edges of the cephalon; it is not always preserved quite symmetrical in relation to the sagittal line. It is not a border furrow but represents the inner edge of the cephalic doublure.

Thorax with smooth axial region, thoracic recess present; anterior segment with short (tr.) pleurae, posterior segment with long, forwardly curved pleurae. Pygidium slightly longer than wide (but length equal to breadth in flattened material), convex, slightly carinate in the anterior half. Faint median node may be visible between a quarter and one-third of the length from front. Border widening slightly posteriorly where it attains about one-ninth of the total length; in life the border sloped down a little but as preserved in shale it lies flat or may even be bent upwards slightly. Moulds of the underside of the border show thin grooves subparallel to the margin and indicate a structure of the doublure which is not interpretable in shale-preserved material.

Fully grown specimens have cephalic and pygidial shields generally from 4·0 to 4·5 mm long and wide, but occasionally reach larger sizes. Meraspid specimens of degree 1 with a cephalic length less than 0·75 mm long show the posterior glabellar lobe faintly outlined all round, most weakly anteriorly (text-fig. 3*a*); it is half or less of the cephalic length, not truncate anteriorly, parallel-sided and two-fifths the width of the cephalon, and has a faint node anterior to its mid-length. There is no cephalic border. The meraspid pygidial axis tapers and reaches to, or nearly to, the posterior border furrow. The border behind the axis is proportionally wider than in the adult, about one-fifth of the pygidial length.

Remarks. The present form agrees with the Westergård's monotype of *C. falanensis* (Pl. 24, figs. 10–12) in proportions and in lateral and posterior profile. Smaller specimens resemble the holotype of *G. bairdi* (Pl. 24, figs. 7–9) which is thought to be a younger growth-stage of the same species and has a more evenly vaulted lateral profile. The present form differs from *G. bituberculatus* because it has no median anterior ridge on the cephalon and the basal lobes become effaced in ontogeny. *G. glandiformis* reaches much greater sizes and its pygidium is not carinate. Comparison with Pokrovskaya's species is inconclusive but the pygidium of *Phoidagnostus angustiformis* (1958, pl. 3, fig. 15) resembles *G. falanensis*. *G.*? *maja* (1958, pl. 4, figs. 9–12) has a narrower thoracic axis and the holotype at least (fig. 10) has a narrower pygidial border. *G. velaevis* has a subquadrate cephalon, a distinct terminal pygidial node, and the pygidial border is wider posteriorly than in *G. falanensis*.

Poulsen and Anderson (1975, p. 2076) suggested that the specimens described above might be referable to *L. laevigata* (Dalman); but no specimens have a cephalic border, and the thoracic axis and pygidial border are too wide for that species. Having examined Scandinavian material of *L. laevigata* preserved in shale and limestone I consider that some at least of Poulsen and Anderson's specimens (1975, pl. 2, figs. 1–9) are wrongly determined: the thoracic axis in their figs. 1 and 7 and the pygidial border in their figs. 7 and 8 are too wide compared with Westergård's (1946) figures. Nor do Poulsen and Anderson's specimens show the posterior of the glabella and front of the pygidial axis, both of which are persistent features in *L. laevigata* (although less so in

L. calva Robison 1964, pl. 83, figs. 1–4), and clearly preserved even when the specimens are flattened in shale.

Occurrence. Mancetter and Outwoods Formations, *laevigata*, *pisiformis*, and *Olenus* Zones. Common at some horizons. In Sweden only one specimen has been found (*pisiformis* Zone). Newfoundland (*laevigata*, *pisiformis*, and *Olenus* zones).

Subfamily AGNOSTINAE McCoy, 1849

Agnostus Brongniart, 1822

Agnostus pisiformis pisiformis (Wahlenberg, 1818)

Plate 24, figs. 15–19

1757 *Entomolithus paradoxus γ pisiformis* Linnaeus, p. 121.
1768 *Entomolithus paradoxus γ pisiformis* Linnaeus, pp. 160–161.
1818 *Entomostracites pisiformis*, Wahlenberg, p. 42, pl. 1, fig. 5.
1958 *Agnostus* (*Agnostus*) *pisiformis* Linnaeus, 1757; Henningsmoen, p. 181, pl. 5, figs. 1–12 [synonymy].
1962 *Agnostus pisiformis* (Linnaeus); Hutchinson, p. 86, pl. 12, figs. 2–6.
1972 *Agnostus pisiformis* (Linnaeus); Taylor and Rushton, pp. 18, 19, pl. 4 [borehole record].

Material. Hundreds of specimens preserved in shale from the Merevale No. 3 Borehole.

Remarks. Some writers have attributed the specific name *pisiformis* to Linnaeus on the strength of the 1757 reference above, which, however, does not make the name available since it predates the 10th edition of *Systema Naturae* (1758); the name does not appear in the latter work, nor in Linnaeus's paper on trilobites (1759). The entry in vol. 3 (Regnum Lapidarum) of the 12th edition of *Systema Naturae* (1768) was ruled invalid in 1954 by I.C.Z.N. Opinion 298. The earliest valid reference seems to be that of Wahlenberg, to whom the species was correctly attributed in Moore 1959, p. O172.

Specimens with rugose cheeks occur (Pl. 24, fig. 18) but as nearly all the specimens are flattened in shale (Pl. 24, fig. 15 is an exception) it is impossible to determine the proportion of such forms. The subspecies *A. pisiformis spiniger* (Dalman) and *subsulcatus* Westergård (1946, pl. 13, figs. 15, 16 and pl. 16, figs. 4, 5, respectively) were not recognized.

Occurrence. In Merevale No. 3 Borehole: fragmentary and poorly preserved specimens probably referable to this species occur sporadically in the Mancetter Formation from 559 ft 7 in. (170·56 m) to the top of the formation; better-preserved specimens occur in the Outwoods Formation from 485 ft 0 in. (147·83 m) to 215 ft 2 in. (65·58 m), being especially abundant towards the top. *L. laevigata* and *A. pisiformis* zones. Scandinavia (same horizons). East maritime Canada (*pisiformis* Zone; also in *laevigata* Zone, judging from the information given by Hutchinson 1962, p. 127, etc.). Siberia (*A. pisiformis–Homagnostus fecundus* Zone; Ivshin and Pokrovskaya 1968). Related subspecies occur in the Mindyallan Stage in Queensland, Australia (Öpik 1967, pp. 96, 98).

Agnostus sp.

Plate 24, fig. 21

1972 cf. *Agnostoglossa*?; Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. One external mould of a complete specimen about 8·5 mm long, BDA 1984.

Remarks. The present specimen resembles some species of *Agnostus* with weak lateral furrows on the pygidial axis, including specimens referred to *A. pisiformis* itself

(Westergård 1946, pl. 13, fig. 11). The cephalon resembles that of *A. pisiformis* (Henningsmoen 1958, pl. 5, fig. 1) but the pygidial axis extends further back towards the border-furrow, is more expanded and rounded behind, and has less distinct lateral furrows than is general in *A. pisiformis*; the pygidial flanks are narrower and the border is broader. It differs from *A. exsulatus* Poulsen (1960, pl. 1, figs. 3, 4) which has a wider cephalon and a shorter and narrower glabella; the pygidium of *A. exsulatus* appears to have a narrower border. *A. artilimbatus* Öpik (1967, pl. 57, figs. 10, 11) has narrower borders and a shorter anterior glabellar lobe. The associated pygidium has a weaker median axial node and also has a terminal axial node (Öpik 1967, p. 97, text-fig. 22).

Species of *Agnostoglossa* Öpik (1967, p. 145) are similar to the present form but differ because there is no preglabellar median furrow, either in the type species *A. bassa* Öpik or in *A. simplexiformis* (Rozova) as figured by Lazarenko and Nikiforov (1968, pl. 2, figs. 1–4).

Occurrence. Uppermost part of the Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, depth 520 ft 0 in. (158·50 m).

Homagnostus Howell, 1935*c* (May)

Remarks. The type species, *Homagnostus obesus* (Belt), is a small agnostid characterized by a relatively long and broad pygidial axis on which the anterior pair of lateral furrows curves inwards and forwards to meet the articular furrow which is of agnostoid type; there is a strong median tubercle extending across the second pair of lateral furrows on to the posterior axial lobe which is rounded behind and does not bear a terminal node. The cephalon has a preglabellar median furrow and a narrow border.

Compared with *Agnostus pisiformis* the shape and furrowing of the pygidial axis are the chief distinguishing features, but *A. pater* Westergård, which has a comparatively smaller axis than *H. obesus*, represents a transitional form.

Forms closely related to *H. obesus* may have the preglabellar median furrow obsolete, for example *H. o. laevis* Westergård (1947) and *H. tumidosus* (Hall and Whitfield) (Palmer 1960, pl. 4, figs. 1, 2). These forms in turn resemble *Rudagnostus* Lermontova, 1951 and *Micragnostus* Howell, 1935*b* (April) which both have a relatively smaller pygidial axis than *H. obesus* and lack a preglabellar median furrow. *Micragnostus* has been treated as a subgenus of *Geragnostus* Howell but the glabella in the type species of *Geragnostus* (*A. sidenbladhi* Linnarsson) is quite distinct (Tjernvik 1956, fig. 27) and the genera are probably unrelated.

For the present I follow Palmer's definition of *Homagnostus* (1960, p. 62) and treat it as a separate genus but its limits are difficult to define exactly as it grades into *Agnostus* and *Micragnostus*, the latter having priority over *Homagnostus*.

Homagnostus aff. *pater* (Westergård, 1930)

Plate 25, fig. 3

aff. 1930 *Agnostus pisiformis pater* subsp. nov.; Westergård *in* Holm and Westergård, p. 9, pl. 1, fig. 1?; pl. 4, figs. 9, 10.
1938 *Proagnostus bulbus* Butts; Resser, p. 48 [*pars*], pl. 10, fig. 21 only.
1972 cf. *Homagnostus obesus* (Belt); Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. One complete external mould 4·4 mm long from Merevale No. 3 Borehole, BDA 1604. Resser's specimen, U.S. National Museum 94867, was kindly loaned by Mr. F. C. Collier.

Remarks. The present specimens resemble *H. pater* (Westergård, 1946, pl. 13, figs. 4–6) from the Andrarum Limestone of Sweden but differ because the pygidial axis is longer and wider; it is nearly half the width of the pygidium and extends back to a transverse line between the bases of the marginal spines, whereas in *H. pater* the axis is about two-fifths the pygidial width, the axis does not extend as far as the marginal spines, and the tubercle on the second axial lobe does not bulge back so strongly. The present form may be distinguished from *H. obesus* (Belt) because the cephalic and pygidial borders are somewhat wider, the posterior glabellar lobe has an elongate (not rounded) median node, the anterior pair of furrows on the pygidial axis curve forwards but do not meet the articulating furrow so distinctly, and because the pygidial axis only just reaches the level of the marginal spines, whereas in a specimen of *H. obesus* of comparable size (Pl. 25, fig. 4) the axis extends further back.

Resser's specimen (1938, pl. 10, fig. 21) agrees with BDA 1604, except that the pygidial axis is slightly broader in proportion; Resser's figure, which is otherwise representative, does not show the left-hand marginal spine which is preserved on the pygidium.

The present form cannot be referred to *P. bulbus* Butts. This binomen was used by Butts (1926, pl. 9, figs. 11, 12) for two specimens he figured but did not describe, one a *Peronopsis*-like pygidium and the other a complete flattened specimen referred by Öpik (1967, pp. 112, 147) to his genus *Agnostascus*. Resser (1938, pl. 10, fig. 17) figured Butts's *Agnostascus*-like specimen and a second complete specimen preserved in chert (fig. 21) which he mistakenly referred to as the 'holotype', even though Butts made no reference to it; the chert-preserved specimen, which is referred to here as *Homagnostus* aff. *pater* is not even available for selection as lectotype of *P. bulbus*. It is evident that the name *Proagnostus bulbus* is available from 1926 (I.C.Z.N. Art. 11) but that the generic concept depends on which of Butts's two specimens is chosen as lectotype; and that *Proagnostus* is no threat to the validity of *Homagnostus* (Öpik 1967, p. 112) but, according to the choice of lectotype, is potentially a synonym of *Peronopsis* (or whatever genus Butts's fig. 11 represents), or a senior subjective synonym of *Agnostascus*.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 393 ft 10 in. (120·04 m). Resser's specimen is from a chert nodule from the Nolichucky Formation, *Cedaria* Zone, of Cedar Bluff, Alabama. Poletaeva and Romanenko (1970, pp. 72, 73) recorded '*Homagnostus bulbus*' from the basal Upper Cambrian of the Altay Mountains, Siberia, but it is not known if their species corresponds to *H.* aff. *pater*.

Innitagnostus Öpik, 1967

Innitagnostus sp.

Plate 24, fig. 20

1972 *Innitagnostus* cf. *neglectus* (Westergård); Taylor and Rushton, p. 9, pl. 4 [borehole record].

Material. A flattened cephalon about 1·8 mm long, BDA 2094. A small pygidium 1·3 mm long (BDA 2153–2154, counterparts) is referred doubtfully to the genus.

Remarks. The cephalon differs from that of *I. neglectus* (Westergård, 1946, pl. 13, fig. 1) because the anterior glabellar lobe is more truncate in front and the lateral furrows are more sharply cut. It appears to have a stronger preglabellar median furrow than *I. innitens* Öpik (1967, pl. 58, fig. 2). Although the present form has weakly scrobiculate cheeks and a small median indentation in the front of the anterior glabellar lobe it cannot be compared closely with *I. tchatertensis* (Kryskov *in* Borovikov and Kryskov 1963, pl. 1, figs. 13, 14) in which these features are strongly developed, together with a pair of distinctive arcuate scrobicules opposite the front of the glabella. The present form compares most closely with cephala assigned to the variable species *I. inexpectans* (Kobayashi) by Öpik (1963, pl. 2, fig. 13; 1967, pl. 63, fig. 2).

The pygidium appears to conform to those of *Innitagnostus* species but the pygidial axis differs from that of *I. inexpectans* in being somewhat pointed posteriorly. It is too small and too badly preserved at the front of the axis to be compared with other species.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, the cephalon at a depth of 558 ft 6 in. (170·23 m) and the pygidium at 574 ft 0 in. (174·96 m). *Innitagnostus* species have been described from the upper part of the *laevigata* Zone to the lower part of the *Olenus* Zone.

Subfamily PTYCHAGNOSTINAE Kobayashi, 1939

Ptychagnostus Jaekel, 1909

Öpik (1961, p. 76) discussed *Ptychagnostus* and its relationship with *Goniagnostus* Howell, 1935*c* which he treated as a subgenus.

Ptychagnostus (*Goniagnostus*) *fumicola* Öpik, 1961

Plate 25, figs. 1, 2

1961 *Ptychagnostus* (*Goniagnostus*) *fumicola* sp. nov.; Öpik, p. 81, pl. 20, figs. 14–17; text-figs. 28, 29, *non* pl. 21, fig. 2.
1967 *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik, 1961; Öpik, p. 91, pl. 57, figs. 1, 2.
1972 *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik; Taylor and Rushton, p. 9, pl. 4 [borehole record as '*Ptychagnostus* cf. *fumicola*'].
1975 *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik; Daily and Jago, p. 540.

Material. One cephalic fragment and one pygidium approximately 3 mm long, BDA 2199, 2201.

Remarks. The cephalic fragment shows only a triangular anterior glabellar lobe, as long as wide, a short lateral lobe behind this, and some radiating marginal scrobiculae. The pygidium agrees most closely with that in Öpik's (1967) plate 57, fig. 2, in the proportions of the divisions of the axis; the specimen in his plate 57, fig. 1 has a shorter terminal portion, and in the holotype (Öpik 1961, pl. 20, fig. 14) the two anterior portions, taken together, are shorter whilst the third portion is longer. The presence of a post-axial longitudinal furrow cannot be established. The external mould of the pygidium shows the base of a marginal spine.

Amongst strongly granulose species of *Ptychagnostus* the present form differs from *P.* (*P.*) *punctuosus* (Angelin) and *P.* (*P.*) *aculeatus* (Angelin) (see Westergård 1946) and *Ptychagnostus* (*P.*) *akanthodes* Robison, 1964, because the posterior part of the pygidium is separated off as in *P.* (*Goniagnostus*) species; furthermore, the pygidial margin has a pair of spines, unlike *punctuosus* and *aculeatus*.

P. aff. *fumicola* (Öpik 1967, p. 91) and *P. nodibundus* Öpik, 1967 (p. 92) are both more closely related but the former has a finer sculpture on the pygidium and the latter has coarser granulation.

Occurrence. Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole at 595 ft 10 in. (181·61 m). Steamboat Sandstone and Mungerebar Limestone, Queensland, Australia (*laevigata* Zone and *torosa-janitrix* Zone).

Family DIPLAGNOSTIDAE Whitehouse, 1936

According to Öpik (1967, p. 81) the Diplagnostidae includes the subfamilies Ammagnostinae, Glyptagnostinae, Pseudagnostinae, Tomagnostinae, Diplagnostinae, Oidalagnostinae, and a few forms not referable to any of these subfamilies. The first four subfamilies need not be considered further here.

Cristagnostus papilio sp. nov., described below, is a modified axiolobate form (Öpik 1967, p. 58) and resembles the Oidalagnostinae (Öpik 1967, p. 134) in having the anterior part of the pygidial axis triannulated and the posterior part of the axis expanded; but it differs in lacking scrobiculae on the flanks and a depression in the pygidial collar. It cannot be referred to the Oidalagnostinae as construed by Öpik, but equally the modified pygidial axis seems inappropriate for the Diplagnostinae. *Cristagnostus* is not, therefore, referred to a subfamily.

Cristagnostus gen. nov.

Name. Cristatus, Latin, crested, and *agnostus*; referring to the longitudinal axial ridge and the pygidial 'crest' or collar.

Type species. Cristagnostus papilio sp. nov.

Other species. Linguagnostus? *reconditus* Poletaeva and Romanenko.

Diagnosis. Diplagnostidae with semi-elliptical cephalon, glabellar rear rounded; anterior part of the pygidial axis short, distinct, divided into three pairs of lateral lobes; this part traversed for its full length by a median ridge which has a pair of knobs side by

EXPLANATION OF PLATE 25

Figs. 1, 2. *Ptychagnostus* (*Goniagnostus*) *fumicola* Öpik, × 12. 1, fragmentary cephalon, BDA 2199 latex. 2, pygidium, BDA 2201. M3, 595 ft 10 in. (181·61 m).

Fig. 3. *Homagnostus* aff. *pater* (Westergård). BDA 1604 latex, × 8. M3, 393 ft 10 in. (120·04 m).

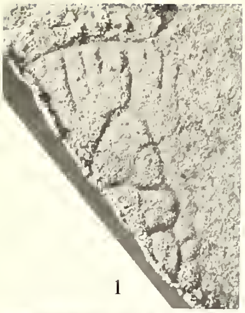
Fig. 4. *Homagnostus obesus* (Belt). TE6 latex, × 8. Trench opposite Old Wharfe Inn, Chilvers Coton, near Nuneaton (SP 3623 9050). Outwoods Formation, *Olenus* Zone.

Figs. 5–13. *Cristagnostus papilio* gen. et sp. nov. 5, holotype, BDA 1320 latex, × 6. M3, 261 ft 6 in. (79·71 m). 6, oblique view of pygidium of holotype, showing posterior median spine (right-hand end of figure), × 20. 7, BDA 1318, × 6. M3, 261 ft 5 in. (79·68 m). 8, 9, small cephala, BDA 1588, 389 ft 6 in. (118·72 m), BDA 1349, 264 ft 7 in. (80·64 m), × 12. M3. 10, BDA 1322 latex, × 6. M3, 261 ft 6 in. (79·71 m). 11, Birmingham University BU 529, × 6. Dumped shale south-west of Cemetery, Hartshill, 4 km north-west of Nuneaton (SP 3241 9408). Coll. Dr. I. Strachan. 12, small pygidium, same exuvia as 8, BDA 1588 latex, × 12. M3. 13, largest pygidium, BDA 1312 latex, × 6. M3, 260 ft 0 in. (79·25 m).

Fig. 14. *Aspidagnostus rugosus* Palmer. BDA 1720, × 12. M3, 435 ft 2 in. (132·64 m).

Figs. 15, 17, 18. *Schmalenseeia amphionura* Moberg. 15, fragmentary thorax and pygidium, BDA 1533, × 12. M3, 374 ft 6 in. (114·15 m). 17, lectotype cranidium, Paleontological Institute, Lund, LO 1660T latex, × 12. Original figured Moberg 1903, pl. 4, fig. 1, Köpingsklint, Borgholm, Öland, Sweden. 18, glabella, BDA 1464, × 25. M3, 277 ft 0 in. (84·43 m).

Fig. 16. *Schmalenseeia* cf. *spinulosa* Lazarenko. Cranidium, BDA 1891, × 14. M3, 485 ft 0 in. (147·83 m).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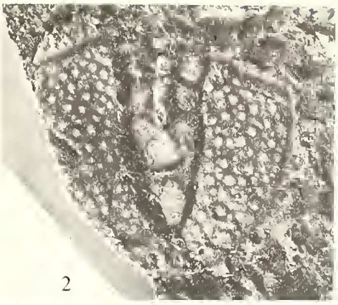
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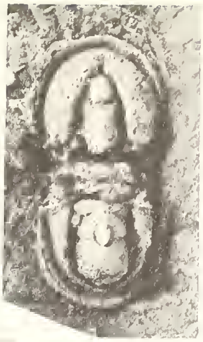
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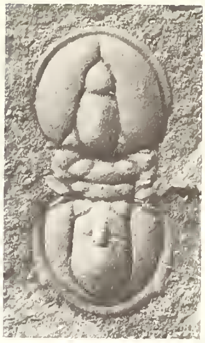
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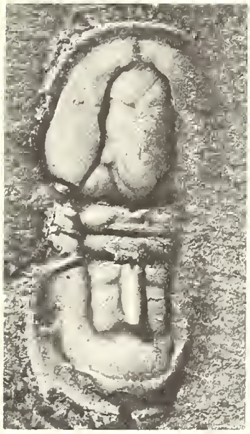
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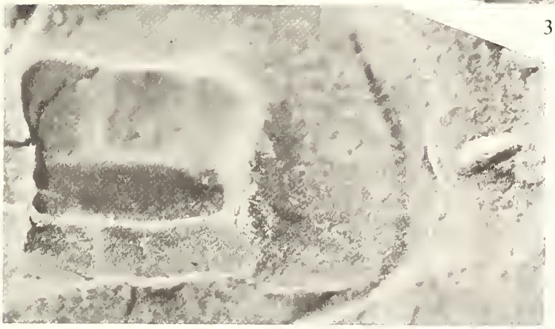
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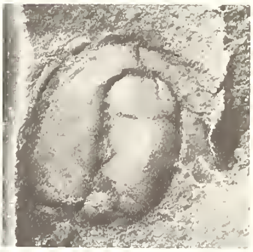
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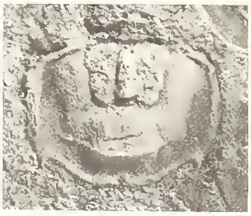
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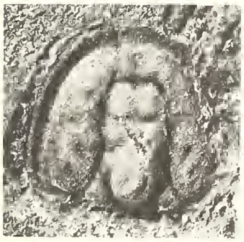
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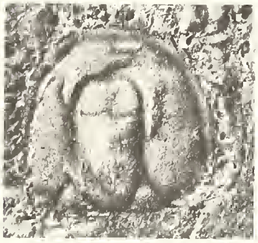
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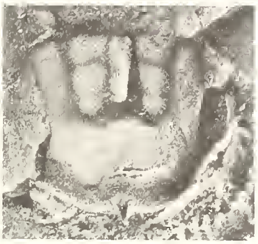
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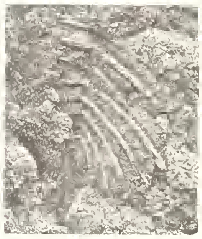
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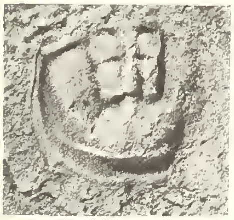
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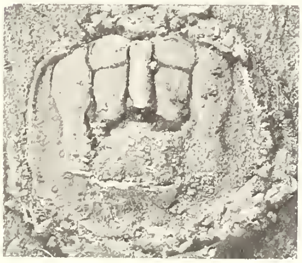
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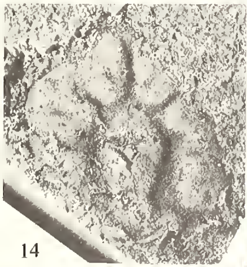
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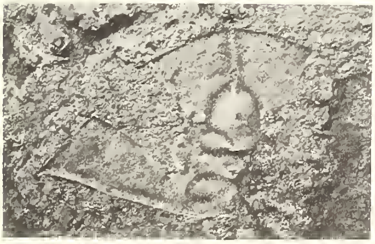
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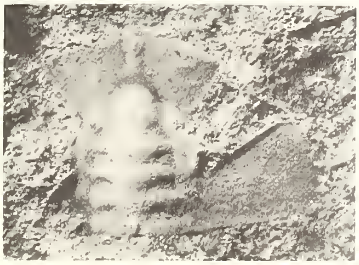
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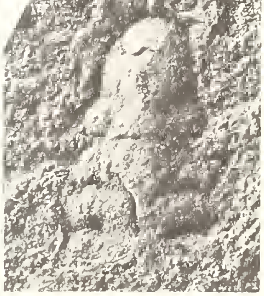
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RUSHTON, Cambrian trilobites

side at its anterior end. Posterior part of axis expanded but obscurely delimited. Pygidial flanks not scrobiculate. Pygidial collar sinuous, uninterrupted, pygidial margin with median notch and median spine.

Remarks. Genera related to the Diplagnostinae and Oidalagnostinae include several species in which the cephala vary little but the pygidia show very diverse features. Genera have been distinguished by combinations of characters such as the development and lobation of the pygidial axis, the presence of scrobicules on the flanks, the presence and development of a pygidial collar, and the development of a median spine on the margin. Most of these features are apt to vary: scrobiculation is present in *Tasagnostus compani* Jago but absent in *T. debori* (Jago 1976, pp. 164, 166); the pygidial collar is present in *Linguagnostus kjerulfi* (Brögger) but absent in *L. groenwalli* Kobayashi (Westergård 1946, pl. 8, figs. 30, 32); and the median spine, though absent in typical forms, may be present in some *Oedorhachis* and *Dolichagnostus* (Öpik 1967, pp. 128, 132). Therefore the genera are most clearly distinguished by the features of the pygidial axis.

In *Cristagnostus* the anterior end of the pygidial axis is comparable with that of *Oidalagnostus* and *Tasagnostus* (Jago 1976, pp. 160–161) but the median ridge differs in being uninterrupted by a cross-furrow. The posterior part of the axis is less well defined and the pygidial collar lies further forward than in those genera. *Cristagnostus* lacks the scrobiculate flanks and the low swellings on either side of the axis in *Oidalagnostus*. The known *Oidalagnostus* species—*O. trispinifer* Westergård 1946, pl. 9, figs. 4–7; *O. personatus* Öpik 1967, pl. 54, figs. 7–9; *O. tienshanicus* Lu (Lu *et al.* 1974, pl. 1, figs. 5–7)—form a well-defined group, so I prefer not to extend it by referring the new form to *Oidalagnostus*.

The semi-elliptical cephalon and advanced pygidial collar of *Cristagnostus* recall those of *Ovalagnostus changi* (Lu *et al.* 1974, pl. 1, fig. 8); but *Ovalagnostus* resembles *Tasagnostus* rather than *Cristagnostus* in the development of the posterior part of the pygidial axis and in the interrupted ridge on the anterior part of the pygidial axis.

The pygidial collar and uninterrupted median ridge of *Cristagnostus* resembles those of *L. kjerulfi* (although the ridge of *Cristagnostus* differs in bearing two knobs at its anterior end). The posterior part of the axis in *Linguagnostus* is, however, small and triangular, indicating an axiolobate structure. I prefer to restrict *Linguagnostus* to axiolobate forms allied to *Diplagnostus* rather than extend it to include the modified axiolobate *Cristagnostus*. No *Linguagnostus* has a median spine on the pygidial margin. The axis of *Plurinodus discretus* Öpik (1967, p. 170, text-fig. 51) is comparable to that of *C. papilio*, but the median ridge is shorter and the furrow behind the axis is not so deep; *P. discretus* has no pygidial collar nor a notched margin. There is some resemblance between the pygidial axial structure of *C. papilio* and the Ordovician form *Galbagnostus galba* (Billings), as figured by Whittington (1965, pl. 4).

The two species referred to *Cristagnostus* are united by two peculiar features: the paired knobs at the anterior end of the longitudinal ridge on the pygidial axis are not known in the Diplagnostinae or Oidalagnostinae, although *Tomagnostus fissus* (Westergård 1946, pl. 7, fig. 29) has a pair of knobs in a comparable position but not on a ridge; and the median pygidial spine springs from a pit in the margin, somewhat as in *Aspidagnostus rugosus* Palmer (1962, pl. 1, fig. 25).

Cristagnostus papilio sp. nov.

Plate 25, figs. 5–13

1962 *Oidalagnostus* cf. *O. trispiniger* [*sic*] Westergard; Hutchinson, p. 80 [*pars*], pl. 7, fig. 20 only.
1972 *Oidalagnostus* sp. nov.; Taylor and Rushton, p. 18, pl. 4 [distribution].

Name. Papilio, Latin, butterfly, fancied resemblance to pygidial axis.

Holotype. BDA 1320–1321 (Pl. 25, fig. 5), an incomplete external mould and counterpart.

Paratypes. A poorly preserved dorsal shield (BDA 1502–1503), a small scattered exuvia (BDA 1587–1588), three cephala (BDA 1311, 1318–1319, 1349), and five pygidia (BDA 1312, 1322, 1579–1580, 1650–1651, Birmingham University BU 529).

Description. Cephalon semi-elliptical, length nine-tenths of width. Glabella three-quarters of cephalic length (slightly less in smaller specimens), about one-third of cephalic width just anterior to basal lobes. Anterior glabellar lobe a little more than one-quarter of glabellar length, indented anteriorly and weakly divided longitudinally in smaller specimens, but rounded in front and with barely a trace of a median depression in full-grown specimens; delimited behind by a weak furrow directed inwards and very slightly backwards. Posterior glabellar lobe parallel-sided with an elongate median ridge on its anterior half. A weak pair of lateral furrows at about one-third from the front of this lobe. The outline of the glabella is 'stepped' to accommodate the basal lobes and is rounded posteriorly. Basal lobes large, triangular, nearly continuous anteriorly with the main glabellar lobe but separated by only a very weak furrow (as in several diplagnostid cephala and also *Peronopsis scaphoa* Öpik, 1961). Acrolobes slightly constricted. Cheeks separated anteriorly by longitudinal preglabellar furrow, with weak scrobiculae. Border furrow broad, border narrow.

Pygidial length, excluding the articulating half-ring, about three-quarters of the width. Articulating furrow of diplagnostid type. Anterior part of axis nearly half of pygidial length, subtrapezoidal, length four-fifths of the width; it narrows slightly posteriorly, is indented medially in front and behind, and is divided into three lobes on either side of the median keel; anterior pair of lobes widen abaxially, second pair longer and roughly square, third pair small, semi-oval, widening abaxially. Median keel has two small knobs, side by side, at anterior end, rises towards the posterior end which is sharply rounded and drops steeply behind. Furrow behind the keel deep and wide. From the posterolateral end of the posterior pair of axial lobes weak furrows extend inwards and slightly backwards to delimit an indistinct transverse lenticular area of weak convexity. On the holotype, but no other specimen, a pair of faint furrows is seen behind this area, close to and parallel with the sagittal line; they may represent the intranotular axis. Behind the anterior part of the axis the axial region is swollen. A sinuous crest (pygidial collar) extends subparallel to, and lies about one-fifth of the pygidial length within, the posterior margin between the marginal spines. Acrolobes constricted. Flanks not scrobiculate. Border furrow wide, border narrow with a pair of posterolateral marginal spines and a median notch from which a tiny spine is directed backwards and downwards (Pl. 25, fig. 6).

Dimensions. The holotype has a cephalon 4·25 mm long and pygidium 3·8 mm long. The largest pygidium is 4·6 mm long.

Remarks. The cephalon of *C. papilio* is very like that of *Diplagnostus planicauda* (Angelin) (Westergård 1946, pl. 8, figs. 22, 24) and, apart from the strong preglabellar median furrow, also like *Oidalagnostus personatus* Öpik (1967, p. 136). It is more rounded in front than *Linguagnostus kjerulfi* and *O. trispinifer.*

The cephalon differs from that of *C. reconditus* (Poletaeva and Romanenko 1970, p. 75, pl. 10, figs. 10–12) from the early Upper Cambrian of the Altay Mountains, Siberia, because the anterior glabellar lobe is longer and shows a tendency to longitudinal division (in smaller specimens). The lateral furrows on the posterior glabellar lobe lie further back in *C. papilio* and the preglabellar median furrow is stronger. The basal lobes of *C. reconditus* are triangular and their anterior ends seem not to be confluent with the glabella.

The pygidium of *C. reconditus* differs from that of *C. papilio* in lacking the weak inwardly and slightly backwardly directed furrows behind the anterior part of the axis. Poletaeva and Romanenko's reconstruction (1970, text-fig. 4) suggests that the pygidial crest bends back to the posterolateral marginal spines and that the median spine is much stouter. Their plate 10, figs. 11 and 12, show that the anterior part of the pygidial axis has three pairs of lobes, the posterior pair with rounded posterolateral corners, and that there are paired tubercles at the anterior end of the axial keel; these are not in their reconstruction.

The pygidium figured by Hutchinson (1962, pl. 7, fig. 20) and referred to *L.*? *reconditus* by Poletaeva and Romanenko has faint furrows extending inwards and backwards behind the axis and a pygidial crest which does not reach the posterolateral spines; by these features it differs from *C. reconditus* and is referable to *C. papilio.*

Occurrence. Outwoods Formation in Merevale No. 3 Borehole, *C. papilio* occurs between 405 ft 8 in. (123·65 m) and 260 ft 0 in. (79·25 m), zone of *Agnostus pisiformis.* One pygidium was collected by Dr. I. Strachan from dumped shales 200 m north of the Royal Oak, Hartshill, by the south-west side of the cemetery (Birmingham University Collection No. BU 529). Newfoundland: above the base of the Elliott Cove Formation, where it is associated with *A. pisiformis* above beds referred to the *laevigata* Zone, as discussed under 'Correlation'.

Family CLAVAGNOSTIDAE Howell, 1937

Aspidagnostus Whitehouse, 1936

Öpik discussed and illustrated *Aspidagnostus* fully (1967, p. 115).

Aspidagnostus rugosus Palmer, 1962

Plate 25, fig. 14

1962 *Aspidagnostus rugosus* n. sp.; Palmer, p. 15, pl. 1, figs. 24–30.
1972 *Aspidagnostus* sp.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. One fragmentary cephalon 2·4 mm long, BDA 1720–1721 (counterparts).

Description. Main part of glabella kite-shaped, contracted behind to nearly half its greatest width which is at the anterior third. Anterior part depressed, pointed in front. Median keel crushed. Basal lobes project laterally at posterior margin. The glabella appears to widen backwards between its narrowest part and the basal lobes, as seen also in one of Palmer's figures (1962, pl. 1, fig. 26); it is possible that this widening represents the anterior part of the composite basal lobe, as in *A. inquilinus* Öpik (1967, pl. 56, figs. 1, 2). Cheeks show longitudinal median furrow and radiating pits and furrows (scrobiculae) nearly symmetrically disposed and very similar in distribution to those of *A. rugosus* (Palmer 1962, pl. 1, fig. 30). Margin not preserved (note that the narrow rim behind the glabella in Pl. 25, fig. 14 is the border of a juvenile *Agnostus pisiformis* underneath the *Aspidagnostus* cephalon).

Remarks. The radiating scrobiculae distinguish this cephalon from those of *A. laevis* Palmer, 1962, *A. lunulatus* (Kryskov, 1963), *A. stictus* Öpik, 1967, and *A. inquilinus* Öpik, 1967. Furthermore, the glabella contracts more strongly posteriorly (in the part between the anterior one-third and two-thirds of its length) than in those species and also *A. parmatus* Whitehouse. However, so far as it is preserved, the present specimen agrees with *A. rugosus.*

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depth 435 ft 2 in. (132·64 m). Conasauga Formation, Alabama, and base of Dunderberg Formation, Nevada, U.S.A., in equivalents of the *pisiformis* Zone and basal *Olenus* Zone (Palmer 1962). Siberia, *A. pisiformis–Homagnostus fecundus* Zone and *Glyptagnostus reticulatus* Zone (Datsenko *et al.* 1968; Ivshin and Pokrovskaya 1968, p. 99; Poletaeva and Romanenko 1970, p. 72).

POLYMERID TRILOBITES

Family MARJUMIIDAE Kobayashi, 1935

Modocia Walcott, 1924*a*

Robison (1964, p. 550) and Rasetti (1965, p. 106) discussed the synonymy of *Modocia* and several other genera, including *Armonia* Walcott and *Perioura* Resser.

Modocia anglica sp. nov.

Plate 26, fig. 20

1972 trilobite n. gen.; Taylor and Rushton, p. 19 [recorded].

Holotype. One specimen in counterpart, RU 2210, well preserved but slightly flattened and crushed. It was prepared so as to show the right fixed cheek and the left free cheek.

Diagnosis. A species of *Modocia* with a smooth exoskeleton, a truncate glabella (not well rounded in front), an occipital tubercle, a backward bend in the anterior border furrow, genal spines in continuity with the margin of the free cheek, a median spine on the axis of the ninth thoracic segment, and a small pygidium with only one distinct pair of furrows.

Description. Cephalic axis three-quarters of cranidial length, sides straight and converging forwards, front not evenly rounded but slightly truncate. Glabella without furrows, width at occipital furrow nine-tenths of length (excluding occipital ring) and one and a half times width between proximal ends of eye-ridges. Occipital ring slightly wider than base of glabella, about one-fifth of glabellar length, simple, with small median tubercle. Frontal area one-quarter of cranidial length, preglabellar field three-quarters as long as anterior border at mid-line. Anterior border furrow makes slight backward bend medially. Width across preocular cheeks about equal to cranidial length. Interocular cheeks (axial furrow to palpebral furrow) about half as wide as glabella at eye-line, but width from axial furrow to ocular margin is two-thirds of glabellar width at eye-line. Palpebral lobe about one-third of length of cephalic axis, placed near mid-length of cranidium. Eye-ridges weak, oblique outwards and backwards, slightly curved. Preocular facial sutures diverge forwards from the eyes at about 30° to sagittal line, and curve sharply inwards at anterior border furrow to cross the anterior border obliquely. Postocular sutures curve out and back from eye to pleuroccipital furrow whence they curve inwards, so that they converge backwards across the posterior border. Postocular cheeks nearly as wide as occipital ring.

Free cheek with stout straight spine nearly as long as remainder of cheek. No genal caeca are visible but a principal genal vein (Öpik 1967, p. 172) extends back from the middle of the eye towards the genal angle. Lateral border slightly narrower than anterior border, striated parallel to margin; anteriorly doublure appears to extend towards mid-line such that rostrum was probably small (tr). Hypostoma unknown.

Thorax of thirteen segments with short pleural spines directed backwards. Anterior axial ring twice as wide as posterior ring. Ninth ring bears a backwardly pointing median spine of unknown length; the other rings lack median tubercles.

Pygidium twice as wide as long. Axis nearly two-fifths of total width, composed of two distinct rings, a faint third ring, and a terminal piece which is rounded behind. Pleural regions with distinct anterior pair of pleural grooves and an indistinct trace of a second pair. Posterior margin rounded, entire. There appears to be a posterior border but this may merely be caused by the edge of the doublure pressed through from below. Doublure sub-parallel to margin, narrows slightly behind axis, striated parallel to margin.

Internal and external surfaces of dorsal exoskeleton smooth. To judge from the convexity shown by the specimen the exoskeleton was thicker and stronger than that of *Olenus* which occurs in the overlying strata (Taylor and Rushton 1972, p. 15, text-fig. 4).

Dimensions. Length of cranidium 6·8 mm; length of cephalic axis 5·1 mm; width of cranidium across eyes 6·9 mm; width of occipital ring 4·0 mm; length of thorax 10·6 mm; length of pygidium 2·2 mm, width 4·4 mm; width of pygidial axis 1·6 mm.

Remarks. This specimen agrees with the description of the genus *Modocia* given by Robison (1964, p. 550) but differs because of the convergence of the posterior ends of the facial suture and the small size of the pygidium; the importance of the former difference is unknown but some other species of *Modocia* (Robison 1964, pl. 87, figs. 19–21) have pygidia relatively as small as that of the present specimen, which is accordingly referred to that genus. It may be distinguished from the type and many other species of *Modocia* (Lochman and Duncan 1944, pl. 11, figs. 35–43; Palmer 1954, pl. 87, figs. 3, 4, 6, 8; Robison 1964, pl. 87, figs. 5–19 and pl. 88, figs. 1–6; Rasetti 1963, pl. 70, figs. 20–25; Rasetti 1965, pl. 1, figs. 13–26 and pl. 2, figs. 1–9) because the glabella is slightly truncate anteriorly, the anterior border has a median backward bend, and the pygidium has only one distinct pair of pleural grooves. Furthermore, apart from *M. yellowstonensis* Duncan, *M.*? *spinosa* Rasetti, and *M. nuchaspina* Robison, none shows an occipital tubercle or spine; and, apart from *M. bidentata* Rasetti and *M. crassimarginata* Rasetti, none of those species has a smooth exoskeleton. *M.*? *agatho* (Walcott) (Rasetti 1965, pl. 1, figs. 27–30) has a more truncate glabella and a suggestion of a median backward bend in the anterior border furrow, which, however, is indistinct; it differs from the English form also because the interocular cheeks are narrower, less than one-third of the glabellar width. The cranidium of *M. elongata* (Walcott) [= *Armonia pelops* Walcott 1924*a*, *b*] is similar to the present specimen but the free cheeks have no spine, the thorax has fourteen segments, and the pygidium has several pairs of pleural grooves. *M. lata* (Howell and Duncan) generally has narrower interocular cheeks and the free cheek has a slender spine which makes an angle with the lateral margin of the cheek (Lochman and Duncan 1944, pl. 15, figs. 29–37). *M.* [*Perioura*] *typicalis* (Resser 1938, pl. 8, figs. 41–43) has fourteen thoracic segments of which the eleventh has long pleural spines, and several pairs of pygidial pleural furrows. The cranidium of *M. masoni* (Resser 1938, pl. 9, figs. 37, 38) is very similar to the English species but the anterior border furrow does not make a conspicuous backward median bend and the figure (Resser's fig. 37) suggests that the surface is granulose. The pygidium (fig. 38, presumably natural size) is 8 mm long yet shows only the anterior pleural and interpleural furrows and is at most weakly furrowed behind; it thus somewhat resembles the English specimen. *M. arctica* Walcott and Resser has a similar pygidium (Lazarenko and Nikiforov 1968, pl. 4, figs. 4–6) but the cranidium has a granulose surface.

Occurrence. Outwoods Formation, top of *pisiformis* Zone, about 15 m below the *Olenus* Zone, Purley Quarry (section No. 5 of Taylor and Rushton 1972, text-figs. 3, 4), about 25 m below the sill. In the U.S.A. *Modocia* species occur in the *Bolaspidella* Zone and *Cedaria* Zone (top Middle Cambrian to base of Upper Cambrian).

Family AGRAULIDAE Raymond, 1913

Cyclolorenzella Kobayashi, 1960

Remarks. According to Kobayashi's diagnosis (1960, p. 389) *Cyclolorenzella* has no glabellar furrows but some species he assigned to the genus show short furrows indenting the sides of the glabella, for example, *C. armata* (Walcott 1913, pl. 14, fig. 17*a*), *C. convexa* (Resser and Endo 1937, pl. 65, fig. 26), and *C. parabola* (Lu) (Chu 1959, pl. 2, fig. 1). The form described below has similar glabellar furrows.

Cyclolorenzella sp.

Plate 26, figs. 1–3

1972 Genus and species undet.; Taylor and Rushton, p. 19, pl. 4 [borehole record].

Material. A cephalon, a cranidium, a juvenile exoskeleton, and a very small pygidium with some thoracic segments (BDA 1565–1566, 1569–1572, 1574–1575); all are incomplete and all show signs of dorso-ventral compression during compaction of the sediment, the smaller specimens being least affected.

Description (based on BDA 1572, the largest specimen). Cephalic axis (excluding occipital spine) two-thirds of cephalic length. Glabella tapered forwards, truncate anteriorly, slightly longer than wide, most elevated at posterior quarter, declining forwards. Posterior glabellar furrows (S1) indent the sides of the glabella at posterior quarter, short; S2 indent sides of glabella near mid-length; creases extending inwards and forwards from S2 appear to be due to compression. S3 not seen. Occipital furrow widest medially, though this may be emphasized by compression. The occipital ring has a peculiar spine: the median part of the occipital ring is raised to form a thin transverse backwardly leaning ridge, which is interpreted as the base of a broad, flattened, occipital spine extending back over the simple posterior edge of the occipital ring, as partly seen in the smallest cephalon (Pl. 26, fig. 3). The spine resembles that of *Toxotis pusilla* Wallerius (Westergård 1948, pl. 3, figs. 17–21). Axial furrow deep. The semicircular depression of the cheeks around the front of the glabella may be partly due to compression. Frontal area is crushed down and slightly crumpled, and is now flat, but seems originally to have been swollen. Ocular ridges transverse, obsolescent laterally, palpebral lobes very indistinct, about one-fifth the length of cephalon. Pleuroccipital furrow wide and deep, shallowing laterally. Postocular cheeks about as wide as occipital ring, with fulcrum at posterior margin about two-thirds the distance from axial furrow to facial suture. Facial suture has a generally backward and outward course but makes an inward bend opposite the eye at two-fifths of the cranidial length from the front; the posterior ends of the facial suture turn inwards across the posterior margin.

The free cheek is narrow, shows no border furrow, but has a short spine continuous with the lateral margin.

The external mould shows that the surface was finely granulose.

The smallest cephalon (Pl. 26, fig. 3) differs from the largest (figs. 1, 2) because its glabella is relatively longer, less tapered, and is rounded anteriorly; the eye-ridges are barely perceptible. The specimen intermediate in size is intermediate in glabellar shape and the strength of the eye-ridges.

EXPLANATION OF PLATE 26

Figs. 1–3. *Cyclolorenzella* sp. 1, 2, crushed cranidium with left free cheek, dorsal and oblique side views. BDA 1572 latex, × 12, 387 ft 0 in. (117·96 m). 3, small exuvia, BDA 1566 latex, × 12, 386 ft 10 in. (117·91 m). M3.

Fig. 4. *Proceratopyge nathorsti* Westergård. Part of cranidium and thorax, RU 132, × 4. Section 5 of Taylor and Rushton (1972, figs. 3, 4), Purley Quarry, north-west of Nuneaton (SP 3060 9608).

Fig. 5. *Aedotes*? sp. Fragmentary cranidium, BDA 1889A, × 25. M3, 485 ft 0 in. (147·83 m).

Figs. 6, 7. *Walcottella* sp. Left valve, BDA 1788, 448 ft 10 in. (136·80 m); right valve, BDA 1825 latex, 466 ft 2 in. (142·09 m). Both × 15. M3.

Fig. 8. *Svealuta primordialis* (Linnarsson). Right valve, BDA 2313, × 4. M3, 639 ft 2 in. (194·82 m).

Figs. 9, 10. *Falites*? *minimus* (Kummarow). Left valves, BDA 1167, 208 ft. 7 in. (63·58 m); and BDA 1452, 275 ft 8 in. (84·02 m). Both × 20. M3.

Fig. 11. *Hesslandona trituberculata* (Lochman and Hu). Right valve, BDA 1817, × 25. M3, 464 ft 6 in. (141·58 m).

Fig. 12. *Falites fala* Müller. Left valve, BDA 1820, × 15. M3, 464 ft 6 in. (141·58 m).

Figs. 13, 14. *Bradoria* sp. Right valve, BDA 1192 latex, 221 ft 2 in. (67·41 m); and left valve, BDA 1826, 466 ft 8 in. (142·24 m). Both × 15. M3.

Fig. 15. *Cyclotron* sp. Left valve, BDA 1409, × 4. M3, 270 ft 6 in. (82·45 m).

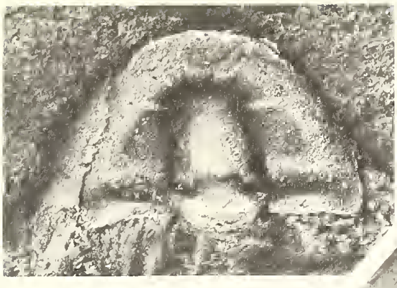
Figs. 16, 17. Hyolithid gen. and sp. undetermined. 16, dorsal and ventral views of conchs, RU 2216, × 3. 17, operculum, counterpart of 16, RU 2215, × 4. Locality as for 4.

Fig. 18. *Lingulella* sp. Pedicle valve, BDA 2162, × 8. M3, *laevigata* Zone, 575 ft 0 in. (175·26 m).

Fig. 19. *Acrothele* sp. Pedicle valve, BDA 2156, × 8. M3, *laevigata* Zone, 574 ft 6 in. (175·12 m).

Fig. 20. *Modocia anglica* sp. nov. Holotype, RU 2210 latex, × 3·3. Locality as for 4.

PLATE 26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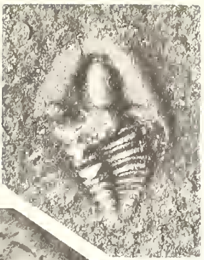
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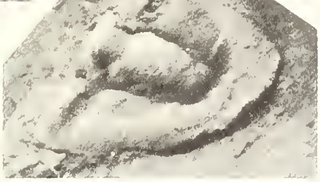
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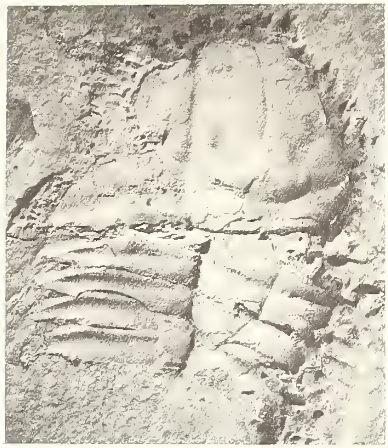
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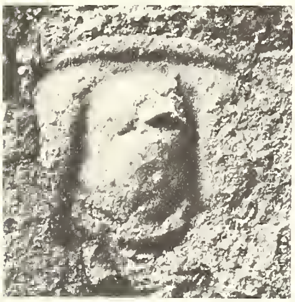
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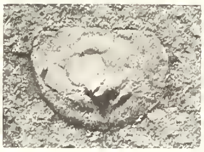
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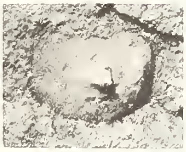
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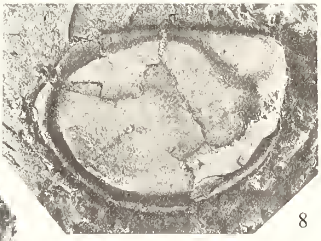
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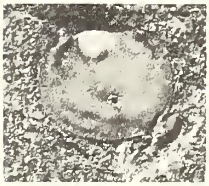
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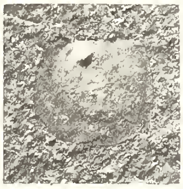
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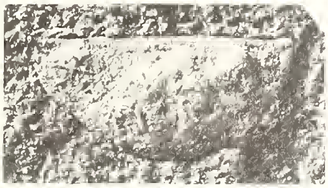
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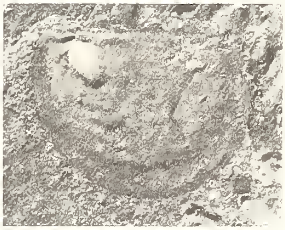
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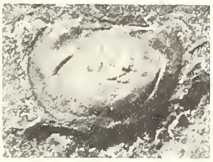
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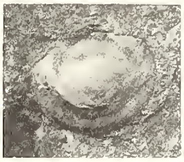
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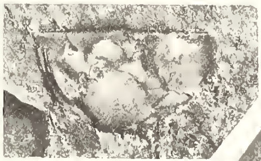
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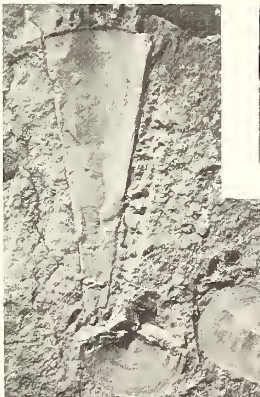
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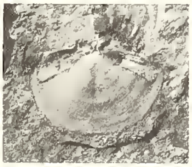
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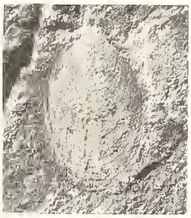
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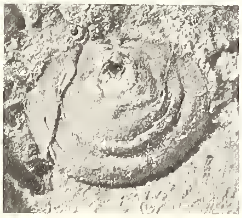
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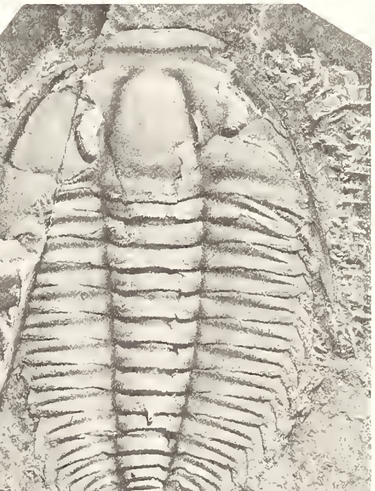
20

RUSHTON, Cambrian shelly faunas

The number of thoracic segments is uncertain but BDA 1566, which is immature and may be incomplete, shows five segments of which the first three at least have axial spines. The pygidium (possibly a transitory pygidium) is poorly preserved but has three axial rings and two or three pairs of pleural grooves.

	BDA 1572 (mm)	BDA 1569 (mm)	BDA 1566 (mm)
Length of cranidium	2·2	—	0·95
Width of cranidium	3·2	1·9	1·4
Length of glabella (without occipital ring)	1·1	0·7	0·6
Width of glabella	1·0	0·5	0·4

Remarks. In recording the occurrence of this form (Taylor and Rushton 1972), I mentioned a fixigenal spine, having overlooked the facial suture shown by the specimen in Plate 26, fig. 3. The specimens are all opisthoparian.

Cyclolorenzella armata (Walcott 1913, pl. 14, fig. 17) has an occipital spine but differs from the present form because the occipital furrow is very weak, the frontal area is longer, and the palpebral lobe is more distinct. *C. tonkinensis* (Mansuy 1915, pl. 2, fig. 13*a–c*) differs in lacking glabellar furrows and the surface is finely and densely pitted. Apart from the occipital spine the present form resembles *C. ogurai* (Resser and Endo 1937, pl. 51, figs. 17–19) and *C. yentaiensis* (Chu 1959, pl. 2, fig. 9) in outline and in having a comparatively weakly inflated frontal area, but it differs in having distinct glabellar furrows and stronger eye-ridges. *C. parabola* (Lu) has free cheeks with tubercles on the margin (Chu 1959, pl. 1, fig. 35). Most other species have narrower postocular cheeks or a strongly granulose exoskeleton.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 387 ft 0 in. and 386 ft 10 in. (117·96 m and 117·91 m). Several species of *Cyclolorenzella* have been described from the Taitzuan and especially the Kushan Formation (Middle–Upper Cambrian) of China and Korea (Chu 1959; Kobayashi 1960, p. 389).

Family LEIOSTEGIIDAE Bradley, 1925
Aedotes Öpik, 1967
Aedotes? sp.

Plate 26, fig. 5

Material. One fragmentary cranidium 1·3 mm long, BDA 1889A.

Remarks. The palpebral lobe is fragmentary but appears to lie at the mid-length of the glabella. The interocular cheek is half as wide as the glabella. The long glabella, the unridged anterior border, and the position of the eye recall *Aedotes*. The glabella reaches nearly to the anterior border, as in *A. instans* Öpik (1967, pl. 21, fig. 3), and has distinct glabellar furrows as in *A. declivis* Öpik and *A. mutans* Öpik (1967, pl. 21, figs. 1, 6). The present specimen differs from all three species because the surface is sparsely but distinctly granulose. The occipital ring is not preserved, so distinction from *Prochuangia mansuyi* Kobayashi (1935, pl. 10, figs. 1–7) depends only on the stronger glabellar furrows shown by the present specimen.

Occurrence. Outwoods Formation, basal layer of the *pisiformis* Zone, at depth 485 ft 0 in. (147·83 m), Merevale No. 3 Borehole. Öpik recorded *Aedotes* from the lower part of the Mindyallan Stage in Queensland; Daily and Jago suggested that this horizon lies just below the base of the Upper Cambrian.

Family BURLINGIIDAE Walcott, 1908
Schmalenseeia Moberg, 1903

Jago (1972) has reviewed the species of *Schmalenseeia.*

Schmalenseeia amphionura Moberg, 1903

Plate 25, figs. 15, 17, 18

1903 *Schmalenseeia amphionura* n.g. et n. sp.; Moberg, p. 96, pl. 4, figs. 1, 2, 3?, 4, 7–10, *non* 5, 6?
1922 *Schmalenseeia amphionura* Moberg; Westergård, p. 119, pl. 1, fig. 19.
1972 *Schmalenseeia* cf. *amphionura* Moberg; Taylor and Rushton, pl. 4 [*pars*], *non* p. 18 [borehole record].

Lectotype. Selected here; Lund University LO 1660T, external mould of a cranidium, figured by Moberg 1903, plate 4, fig. 1; a cast is figured here, Plate 25, fig. 17.

New material. Four fragments showing the cephalic axis and parts of the frontal area; two fragmentary pygidia, one with two thoracic segments. BDA 1463, 1463A, 1464, 1532–1533.

Remarks. The syntypes of *S. amphionura* are preserved in limestone and are distinctly convex, the cranidia being about one-quarter as high as long and the greater part of the convexity being due to the down-sloping cheeks; but the exoskeleton is very thin and it is to be expected that if specimens become flattened the postocular cheeks, whose posterior margins are straight and nearly transverse when preserved in limestone (Pl. 25, fig. 17), might then be bent forwards from the base, their weakest part (cf. Pl. 25, fig. 16). Therefore the forward curvature of the posterior cranidial margin is not a reliable criterion for specific distinction unless reference is made to the state of preservation of the specimens.

Four cranidia from Moberg's material show that in some specimens the glabella tapers forwards more than in Westergård's figure. The longitudinal preglabellar ridge varies in strength but does not extend back on to the frontal glabellar lobe. All the specimens have an occipital tubercle though it is very weak in the smallest specimen (1·25 mm long), and all have a weak pleuroccipital furrow which fades out laterally (Moberg 1903, pl. 4, figs. 1, 2) or extends to the genal angle. The palpebral lobes are raised and the edge of the cranidium is turned up along the preocular and postocular sutures (Pl. 25, fig. 17) so that the free cheek may have been raised above the level of the fixed cheek. These upturned edges make the course of the sutures especially clear, even in shale-preserved specimens.

The cephalic fragments from Merevale No. 3 Borehole have a tapering glabella (1·0 to 1·4 mm long), and an occipital tubercle, but differ from *S. spinulosa* Lazarenko in having no other glabellar tubercles. The anterior glabellar lobe lacks the median ridge shown by *S. gostinensis* Jago. The pleural tips on the figured pygidial fragment seem slightly more pointed than in Westergård's figured specimen, an external mould of a small individual.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, the cephalic fragments at a depth of 277 ft 0 in. (84·43 m) and the figured pygidium at 374 ft 6 in. (114·15 m); lamprophyre sills are intruded between these two horizons and their corrected stratigraphical separation is estimated to be about 10 m. In Sweden *S. amphionura* occurs at the base of the *pisiformis* Zone (Westergård 1948, p. 3).

Schmalenseeia cf. *spinulosa* Lazarenko, 1960

Plate 25, fig. 16

cf. 1960 *Schmalenseeia spinulosa* sp. nov.; Lazarenko, p. 253, pl. 53, fig. 18.
1972 *Schmalenseeia* cf. *amphionura* Moberg; Taylor and Rushton, p. 18, pl. 4 [*pars*] [borehole record].

Material. A flattened cranidium 1·7 mm long (BDA 1890–1891) and several fragments, chiefly thoracic segments (BDA 1886A, 1887A–D, 1888–1889).

Remarks. S. spinulosa is distinguished especially by the median tubercles or spines on the glabella; Dr. J. B. Jago kindly lent me an enlarged photograph of the holotype of *S. spinulosa* which shows a tubercle and a trace of a longitudinal median ridge on the anterior glabellar lobe (L4). Each of L3, L2, and L1 are drawn up to form tubercles, and are also drawn backwards, so that in the case of L1 the tubercle lies opposite the occipital furrow. The cranidium figured here has tubercles opposite the occipital furrow, at the posterior edge of L2, and possibly a small one on L3 but one cannot be sure because the exoskeleton is crumpled there. The figured cranidium shows a thin longitudinal ridge on L4 continuous with the preglabellar ridge; this is probably an original feature but it is slightly irregular and it appears to have been accentuated by crumpling. No median node can be distinguished on L4 on this specimen but a fragmentary glabella on the same slab has a weak median node on L4 and shows the preglabellar ridge extending back on to L4 and quickly dying out without reaching the node. Apart from possible differences in the development of the glabellar tubercles the present form differs slightly from *S. spinulosa* because the preglabellar field is a little shorter (0·30 of the cranidial length compared with nearly 0·35 in *S. spinulosa*) and the anterior glabellar lobe is a little larger; but as the holotype of *S. spinulosa* is a larger specimen (cranidium 2·7 mm long) the importance of these differences is uncertain.

The proportions of the present cranidium agree closely with those of *S. amphionura* but the latter species has no glabellar spines (other than an occipital spine).

The clearest distinction of *S. gostinensis* Jago (1972) from the form figured here is the absence of a spine or tubercle on L2, but the sigmoidal curvature of the pleuroccipital furrow and the strong longitudinal ridge on L4 (Jago 1972, pl. 44, figs. 19–21) may also represent original differences. Judging from Jago's figures the cephalic axis is less than one-fifth of the cranidial width (not one-third as given by Jago on p. 234), narrower than that of *S. spinulosa* which is about one-quarter of the cranidial width. The glabella of *S. gostinensis* appears also to taper less strongly forwards but this may be because the specimens are comparatively small (the glabella of *S. amphionura* tends to taper less strongly in smaller specimens).

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, at depth 485 ft 0 in. (147·83 m). *S. spinulosa* was described from the *pisiformis* Zone of the middle reaches of the River Olenek, on the North Siberian Platform.

Family CERATOPYGIDAE Linnarsson, 1869
Proceratopyge Wallerius, 1895
Proceratopyge nathorsti Westergård, 1922

Plate 26, fig. 4; text-fig. 3*b*

1922 *Proceratopyge nathorsti* n. sp.; Westergård, p. 120, pl. 2, figs. 3–5.
1947 *Proceratopyge nathorsti* Westergård; Westergård, p. 10, pl. 2, figs. 2–7.
1958 *Proceratopyge nathorsti* Westergård 1922; Henningsmoen, p. 186, pl. 7, figs. 2, 3 [further synonymy].
1972 *Proceratopyge nathorsti* Westergård; Taylor and Rushton, p. 15, text-fig. 4 [recorded].

Material. A fragmentary cranidium with a tapered glabella and with some thoracic segments, RU 132; a small fragmentary pygidium, RU 122.

Remarks. The fragments illustrated here are distinguished from *P. conifrons* Wallerius (Westergård 1947, pl. 1, figs. 7–16) because the glabellar furrows are weaker and the pygidium is less transverse. *P. similis* Westergård (1947, pl. 2, fig. 1) has more nearly triangular postocular cheeks whereas those of *P. tullbergi* Westergård (1947, pl. 2, fig. 8) are more transverse ('strap-like'). *P. liaotungensis* Kobayashi and Ichikawa (1955) has no glabellar node and the occipital ring is thickened medially. *P. nectans* Whitehouse 1939 (see Henderson 1976) appears to have weaker glabellar furrows. No comparison is made with the many species of *Proceratopyge* which have a long pygidium or a parallel-sided glabella.

Occurrence. Outwoods Formation, *pisiformis* Zone, and possibly basal *Olenus* Zone, just below the lowest *Olenus* at Purley Quarry (Taylor and Rushton 1972, text-fig. 4, p. 15). *A. pisiformis* Zone and possibly base of *Olenus* Zone in Sweden. *A. pisiformis* Zone in Oslo district, Norway. *A. pisiformis–Homagnostus fecundus* Zone, River Lena, Siberia (Ivshin and Pokrovskaya 1968, p. 98).

CRUSTACEA
Order BRADORIIDA Raymond, 1935

This group of ostracod-like crustaceans has been studied recently by Fleming (1973) and Kozur (1974) who cite earlier work on the group. Kozur regarded the Bradoriida as forerunners of the Ostracoda, and stated that most of the Phosphatocopina of Müller (1964) cannot be distinguished from the Bradoriida; however, the genus *Hesslandona* Müller, 1964, which has a median dorsal plate (somewhat like the phyllocarid *Rhinocaris*), was excluded from the Ostracoda. Müller (1975, p. 178) has contested the basis of Kozur's conclusions. The shale-preserved material from the Nuneaton district yields no evidence contributory to this debate, but Kozur's classification is followed here for the present.

Superfamily BRADORIACEA Matthew, 1902
Family BRADORIIDAE Matthew, 1902
Bradoria Matthew, 1899
Bradoria sp.

Plate 26, figs. 13, 14

Material. Two figured valves, BDA 1192 and 1826, are assigned to *Bradoria* but some juvenile specimens may also belong here.

Description. Valves convex, without definitely distinguishable nodes. Dorsal margin straight, four-fifths of greatest length of valve. Cardinal angles obtuse. Anterior, ventral, and posterior margins form an unbroken curve, curvature strongest just below anterodorsal angle. Greatest height is three-quarters of the length and is placed at or just behind the mid-length. No marginal rim. Surface smooth.

Remarks. This form of *Bradoria* has a nearly symmetrical outline and the ocular node is absent or inconspicuous; it thus differs from most species but may be compared with *B. cambrica* (Matthew) (Ulrich and Bassler 1931, pl. 3, fig. 15) which is a little higher and has a punctate surface. *B. hicksii* (Jones) is a little longer and has more rounded cardinal angles. Andres (1969, p. 175) figured a similar but less symmetrical *Bradoria* sp. from the middle Middle Cambrian of Sweden.

Occurrence. Outwoods Formation, near the base and top of the *pisiformis* Zone, Merevale No. 3 Borehole, depths 466 ft 8 in. (142·24 m) and 221 ft 2 in. (67·41 m).

Walcottella Ulrich and Bassler, 1931
Walcottella sp.

Plate 26, figs. 6, 7

Material. Two specimens, BDA 1788 and 1825, are assigned to *Walcottella* but some juvenile and poorly preserved specimens may also belong here.

Description. Dorsal edge straight, four-fifths of greatest length of valve. Cardinal angles obtuse. Anterior, ventral, and posterior margins form a smooth curve. Greatest height nearly three-quarters of greatest length and placed just behind the mid-length. A strong tubercle is placed at the mid-length but well below the mid-height. Surface smooth.

Remarks. Of the thirteen species of *Walcottella* described by Ulrich and Bassler (1931) the present specimens most resemble *W. concentrica* which is a short species with the median tubercle subcentrally placed. It differs from this and all the other species because the surface is not punctate or reticulate (despite the preservation in shale, such detail should be visible if it was present originally).

Occurrence. Rare in the Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 466 ft 2 in. (142·09 m) and 448 ft 10 in. (136·80 m). All Ulrich and Bassler's species are from the Bright Angel Shale (Middle Cambrian) of Bass Canyon, Arizona, U.S.A.

Genus FALITES Müller, 1964
Falites fala Müller, 1964

Plate 26, fig. 12

1964 *Falites fala* n. sp.; Müller, p. 25, pl. 3, figs. 3–10; pl. 5, fig. 6.
1972 *Falites* sp.; Taylor and Rushton, p. 13.

Material. The description is based on a flattened left valve 1·85 mm long, BDA 1820. A few isolated valves are referred to this species (BDA 1824, 1844, 1855, 1863) but numerous imperfect valves may represent this or another species.

Description. Outline more than a semicircle. Dorsal edge straight, about five-sixths of maximum length. Anterodorsal angle a little more than 90°; posterodorsal angle very obtuse. Anterior, ventral, and posterior margins form a smooth curve. Greatest height at the mid-length, about three-quarters of the maximum length; the height is slightly less than the length of the hinge and lies at about its posterior one-third. Weakly marked border, narrow anteriorly, widening to nearly one-fifth of the total height ventrally and narrowing slightly posteriorly. One distinct node, just below hinge, at one-quarter of the length from the anterior end. No other nodes visible.

Remarks. This specimen agrees with Müller's description and figures (especially his pl. 3, fig. 6) but the anterior node seems to lie a little higher and further back. There is no trace of the two fainter nodes seen below the middle and posterior of the dorsal margin in some specimens (Müller 1964, pl. 5, fig. 6). The marginal rim on the present material is accentuated, probably because it reflects the edge of the duplicature.

Compared with *F. fala*, *F. angustiduplicatus* Müller has a narrower duplicature (narrower than one-tenth of the maximum height) and the posterodorsal angle is hardly more obtuse than the anterodorsal angle. *F. cycloides* Müller is slightly shorter, the height being four-fifths of the length, and the dorsal margin is about equal to the height. *F.*? *minimus* is discussed below.

Occurrence. In the Nuneaton district *F. fala* is rare in the Outwoods Formation, *pisiformis* Zone (481 ft 6 in. (146·76 m) to 464 ft 6 in. (141·58 m) in Merevale No. 3 Borehole) and occurs also rarely in the Monks Park Formation, between the *Leptoplastus angustatus* Subzone and *Ctenopyge postcurrens* Subzone (Taylor and Rushton 1972, pp. 25, 29, 30). Müller (1964, p. 37) recorded *F. fala* from the *pisiformis* Zone and the *Peltura* zones in Sweden.

Falites? *minimus* (Kummerow, 1931)

Plate 26, figs. 9, 10

1928 *Aristozoe*? cf. *primordialis* Linnss sp.; Kummerow, p. 42, pl. 2, fig. 19.
1931 *Aristozoe*? *minima* n. sp.; Kummerow, p. 255, fig. 18.
1964 *Falites*(?) *minima* (Kummerow, 1931); Müller, p. 29, pl. 4, figs. 8–12, 16.
1972 *Falites*? *minimus* (Kummerow); Taylor and Rushton, p. 13, pl. 4 [borehole record].

Material. Of four flattened valves, BDA 1167–1168, 1276–1277, 1452–1453, 1771, and 1774 (counterparts), two left valves are figured.

Description. Outline horseshoe shaped, nearly symmetrical about a dorsal to ventral line, height about seven-eighths of length; dorsal edge three-quarters of total length, and six-sevenths of the height. Anterior, ventral, and posterior margins make an even curve, slightly trapezoidal in aspect. Antero- and posterodorsal angles nearly equal, both a little over 90°. Node below dorsal margin, just forward of the mid-length. Flattened marginal zone indistinct, but suggestive of a duplicature of width about one-fifth of the total height. BDA 1452 is 0·78 mm long and 0·71 mm high; BDA 1167 is 0·82 mm long and 0·68 mm high.

Remarks. This form is distinguished from *F. fala* and *F. angustiduplicatus* by the relatively high valves. *F. cycloides* has high valves but the shape is generally less symmetrical and the anterior node is further forward.

Occurrence. In the Nuneaton district confined to the *pisiformis* Zone, in the Outwoods Formation, Merevale No. 3 Borehole, depths 446 ft 0 in. (135·94 m) to 208 ft 7 in. (63·58 m). Müller recorded this species from the *pisiformis*, *Olenus*, and *Peltura minor* zones in Sweden.

Superfamily HIPPONICHARIONACEA Sylvester-Bradley, 1961
Family HIPPONICHARIONIDAE Sylvester-Bradley, 1961
Cyclotron Rushton, 1969
Cyclotron sp.

Plate 26, fig. 15

1972 *Cyclotron* aff. *angelini* (Barrande); Taylor and Rushton, p. 18, pl. 4 [distribution].

Material. A large but slightly crumpled left valve, 6·3 mm long and 3·4 mm high (BDA 1408–1409); also a right valve and a fragmentary specimen (BDA 1254, 1261).

Remarks. The large undivided swelling low in the middle of the valve distinguishes the present form from *C. lapworthi* (Groom, 1902, p. 84, pl. 3) and *C. marginatum* (Ulrich and Bassler, 1931, pl. 8, figs. 28, 29). *C. angelini* (Barrande) has sharper cardinal angles and the node at the posterodorsal corner is weaker (Westergård 1947, pl. 1, fig. 15); the node low down in front is rounded in *C. angelini*, not elongated towards the anterodorsal corner as in the present form. *C. nodomarginatum* Schrank (1973, pl. 3, fig. 2) differs in having large posteroventral nodes projecting beyond the free margin: although the figured specimen is not well preserved in this region it seems improbable that it had such nodes originally.

Occurrence. Rare in the Outwoods Formation, upper part of the *pisiformis* Zone, Merevale No. 3 Borehole, depths 270 ft 6 in. (82·45 m), 252 ft 6 in. (76·96 m), and 252 ft 4 in. (76·91 m).

Family BEYRICHONIDAE Ulrich and Bassler, 1931
Svealuta Öpik, 1961
Svealuta primordialis (Linnarsson, 1869)

Plate 26, fig. 8

1869 *Leperditia primordialis* n. sp.; Linnarsson, p. 84, pl. 2, figs. 65, 66.
1931 *Aluta primordialis* (Linnarsson); Ulrich and Bassler, p. 59, pl. 8, figs. 11, 12 [synonymy].
1944 *Aluta primordialis* (Linnarsson); Westergård, p. 33 [distribution in Scanian borings].
1961 *Svealuta primordialis* (Linnarsson); Öpik, p. 174, text-fig. 58.
1972 *Svealuta primordialis* (Linnarsson); Taylor and Rushton, p. 8, pl. 4 [borehole record].

Material. The internal mould of a crushed right valve with scraps of the exoskeleton remaining (BDA 2313) is figured. Two further fragmentary left valves (BDA 2394, 2395).

Description (after Linnarsson). Equivalved, strongly convex, oblong, very broad in the middle; border depressed, obsolescent anterodorsally. Dorsal margin straight, occupying three-quarters of the length, making an angle with the posterior margin; evenly curved ventrally, confluent without angulation anteriorly. Each valve divided by indistinct grooves into three swollen parts, the posterior one large and ovate, the anterior ones small, the upper one subtriangular, the lower one globose, inflated, projecting beyond the margin. Ocular tubercle undifferentiated. Exterior of valve may either be smooth or finely granulated. Length 8 mm, height 5 mm.

Remarks. The specimen figured here is 8·2 mm long and 6·2 mm high; this is proportionally higher than Linnarsson's figured specimen, partly because it is 'spread' by crushing and partly because the anteriorly projecting node is broken off, reducing the length. The upper of the anterior nodes is one-third of the length and one-third of the height of the valve. The groove marking it off passes into the dorsal border furrow. The dorsal margin is three times as long as the short posterodorsal margin. Ventrally the width of the border is less than one-tenth of the height of the valve. The main body is rounded posteriorly as in Linnarsson's figure, not angulate as in Öpik's reconstruction (1961) and also the elongated valve of *S.* cf. *primordialis* (Öpik 1967, pl. 2, fig. 2).

Occurrence. In Britain, known only from the lower part of the Mancetter Formation, *laevigata* Zone, Merevale No. 3 Borehole, 700 ft 0 in. (213·36 m) and 639 ft 2 in. (194·82 m). In Sweden *S. primordialis* is recorded from the *laevigata* Zone in Scania (Westergård 1944, p. 33; 1946, p. 11) and Västergötland (Wallerius 1930, p. 50). Öpik (1961, p. 175) stated that it also occurs abundantly in the *Solenopleura brachymetopa* Zone, but gave no bibliographic reference to such a record.

CRUSTACEA INCERTAE SEDIS

Hesslandona Müller, 1964

Remarks. Hesslandona is characterized by a dorsal median plate with a hinge along both its edges—a structure distinct from all ostracods but comparable with the ephippia of Cladocera (Adamczak 1965). *Hesslandona* was excluded from the Bradoriida by Kozur (1974).

Hesslandona trituberculata (Lochman and Hu, 1960)

Plate 26, fig. 11

1960 *Dielymella*? *trituberculata*, n. sp.; Lochman and Hu, p. 826, pl. 98, fig. 56.
1972 *Vestrogothia* sp.; Taylor and Rushton, p. 18 [*pars*].

Material. Four right valves and one left valve (BDA 1476, 1479, 1782, 1785, 1817). Several poorly preserved and juvenile valves may also be referable to this species.

Description. Height about half the length, greatest height just anterior to the mid-length. Dorsal edge straight. Anterior cardinal angle about 80°. Anterior and ventral margins evenly curved, lowest point of venter may be more sharply curved. Posteroventral margin nearly straight, posterior truncated obliquely downwards and forwards. Middle of valve slightly swollen, posterior end nearly flat. There are three low knobs at about one-fifth of the total height below the hinge-line, at one-fifth, two-fifths, and four-fifths of the total length from the front. Surface smooth. The smallest specimen (1·43 mm long) is proportionally slightly less high. One specimen (BDA 1814) and a few of the immature specimens show the median plate but do not show spines coming off this plate.

Remarks. In the present specimens the three knobs lie on a straight line as in *H. trituberculata* but not as in *H. necopina* (Müller 1964, pl. 1, fig. 2). The outline is more elongated than in *H. kinnekullensis* Müller.

Occurrence. Outwoods Formation, *pisiformis* Zone, Merevale No. 3 Borehole, depths 464 ft 6 in. (141·58 m) to 281 ft 10 in. (85·90 m). The holotype is from the Du Noir Limestone (early Upper Cambrian, *Cedaria* Zone) of the Sheep Mountain Section, Wyoming (Lochman and Hu 1960).

MOLLUSCA
Class HYOLITHA Marek, 1963
Order HYOLITHIDA Matthew, 1899
Hyolithid gen. et sp. undetermined

Plate 26, figs. 16, 17

Remarks. Of the hyolithids present those from the top of the *pisiformis* Zone at Purley Quarry (Nos. RU 2212–2216, 2218–2240) are best preserved. The conchs are flattened, so the cross-section and details of the lateral edges are unknown. The apical angle (as preserved) is 20° and the surface is marked only by growth lines which show a rounded ventral edge and transverse dorsal edge (Pl. 26, fig. 16). The opercula show a conical shield (Marek 1963, text-figs. 1, 2) with one pair of clavicles, but the cardinal shield is too poorly preserved for details other than a trace of the paired cardinal processes to be made out. Long curved appendages ('helens', Runnegar *et al.* 1975) are associated but show little detail apart from faint longitudinal (but not transverse) striae. The preservation is insufficient for the species or genus to be determined but the form appears to be related to the family Hyolithidae.

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FAUNAL SUCCESSION AND MODE OF LIFE OF SILURIAN GASTROPODS IN THE ARISAIG GROUP, NOVA SCOTIA

by JOHN S. PEEL

ABSTRACT. Three basic types of Silurian gastropod faunas are recognized in the near-shore deposited Arisaig Group, Nova Scotia. A hard-bottom, shallow marine platform fauna is characterized by trochiform pleurotomariaceans. A soft-bottom, shallow marine platform fauna has dominant high-spired gastropods, and lacks the trochiform pleurotomariaceans. A more off shore, soft-bottom, open-lagoon fauna is typically composed of trochiform holopeids, although these give way to small bellerophontaceans in shallower water. Morphologically similar, but taxonomically different, faunas reoccur with repetition of environments in successive regressive sedimentary phases.

High-spired gastropods and explanate bellerophontaceans show morphological adaptations to life on a soft bottom. Trochiform pleurotomariaceans were associated with a harder bottom, while many other Arisaig gastropods were probably algal foliage dwellers.

SILURIAN gastropods from the near-shore deposits of the Arisaig Group, Nova Scotia (text-fig. 1) followed a number of modes of life reflecting differences in the environments in which they lived. The modes of life are to a large extent inferred from interpretations of shell functional morphology. However, the nature of the enclosing sediment and the gross size of individual gastropods provide additional discriminating characters which are particularly important to the evaluation of algal-foliage supported modes of life.

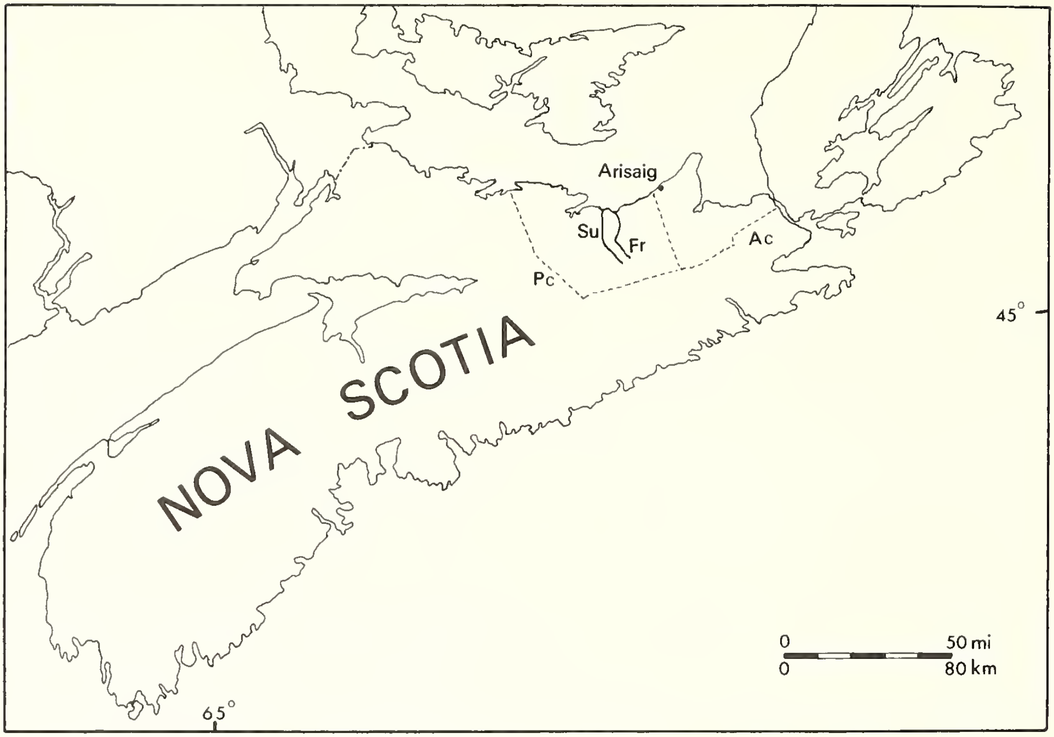
Three basic gastropod faunas within the Arisaig Group are related to specific bottom conditions and distance from shore. Each faunal grouping is characterized by distinct gastropod morphotypes. The faunas are repeated in successive regressive phases during the depositional history of the sequence, although few species persist from one regressive phase to the next. The re-establishment of morphologically similar, but taxonomically dissimilar, gastropod faunas with the repetition of comparable sedimentary environments suggests strong correlation between shell form in Arisaig gastropods and the physical environment.

THE GASTROPOD FAUNA

Gastropods were first described from the Arisaig Group by Hall (1860) who named two characteristic high-spired murchisoniids, *Murchisonia* (*M.*) *aciculata* and *M.* (?*Hormotoma*) *arisaigensis*, and the still unique specimen of *Onychochilus*(?) *reversa*. Dawson (*in* Honeyman 1860) supplied notes on several common species but without illustration. The general faunal monograph of McLearn (1924) included eighteen species of gastropods, of which six species and one variety were new. A recent series of papers by Peel (1974; 1975*a*–*c*; 1977) has increased this total to more than sixty species and provides the taxonomic base for the present paper (text-fig. 2).

The trilobed bellerophontaceans *Plectonotus* and *Tritonophon* (Pl. 27, figs. 3, 8, 20) are represented by five species distributed throughout the sequence (text-fig. 2).

[Palaeontology, Vol. 21, Part 2, 1978, pp. 285–306, pl. 27.]

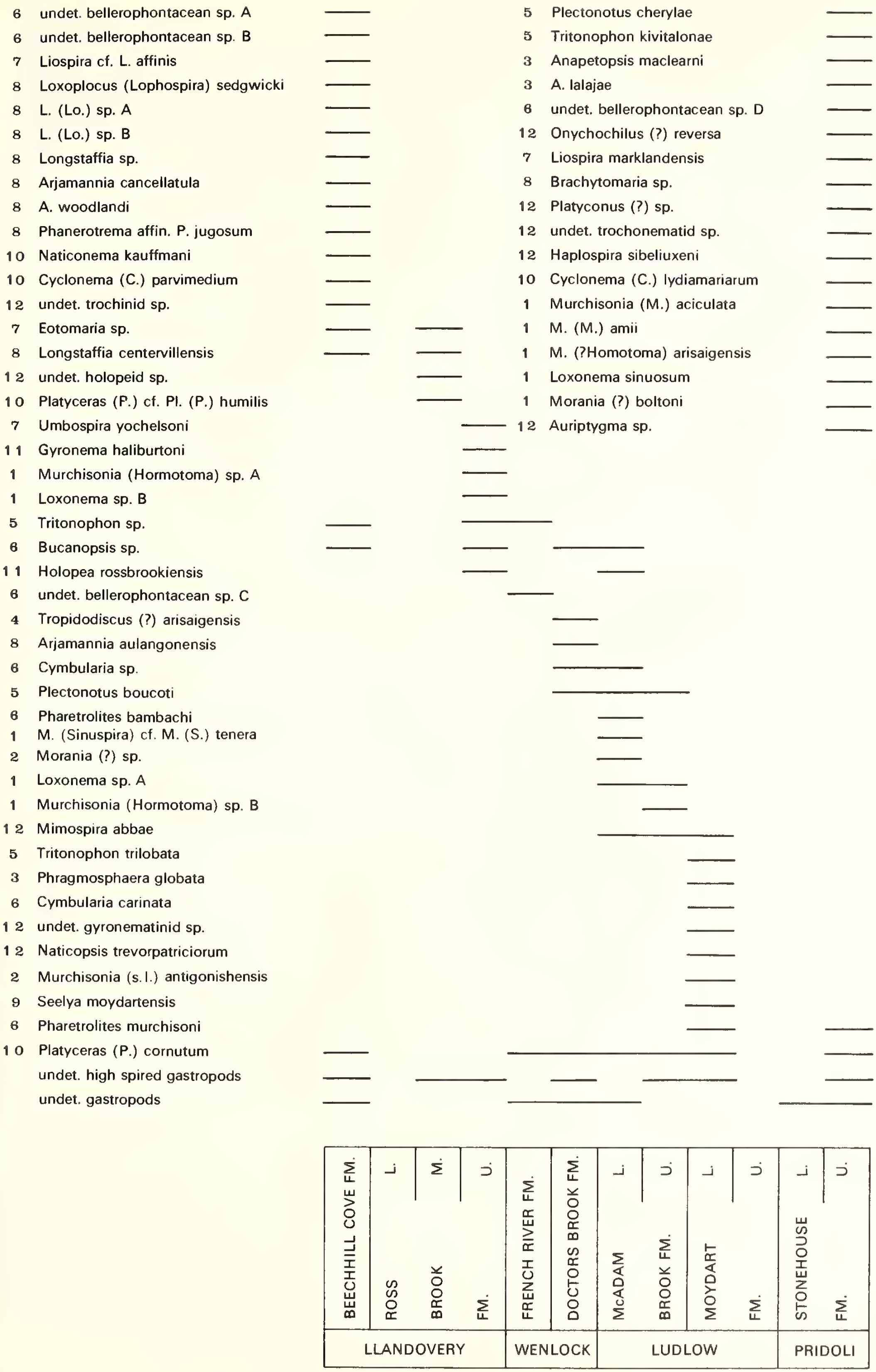


TEXT-FIG. 1. The Arisaig region, Nova Scotia. Ac, Antigonish County; Pc, Pictou County; Fr, French River; Su, Sutherland River.

Trochiform pleurotomariaceans (Pl. 27, figs. 15, 18, 22) dominate the Beechhill Cove Formation (*Loxoplocus*, *Arjamannia*, *Longstaffia*, *Phanerotrema*) but also occur rarely in other formations. The trochiform holopeids *Holopea* and *Gyronema* (Pl. 27, figs. 1, 4) are abundant in the Ross Brook Formation and the former reappears in the McAdam Brook Formation. High-spired murchisoniids (Pl. 27, figs. 14, 19) and loxonemataceans (Pl. 27, figs. 11, 16) are frequently abundant and dominate in the lower Moydart and upper Stonehouse formations. Other characteristic elements include trochiform platyceratids (Pl. 27, figs. 2, 23), explanate bellerophontaceans (Pl. 27, fig. 5), lenticular pleurotomariaceans (Pl. 27, figs. 7, 9, 13), a trochiform murchisoniacean (Pl. 27, fig. 10), and several small bellerophontaceans (Pl. 27, figs. 12, 17, 21).

This gastropod fauna shows great similarity to contemporaneous faunas from level-bottom communities in the Silurian of Britain described by Sowerby (*in* Murchison 1839), Longstaff (1924), Straw (1933), and Pitcher (1939). Gastropod faunas from Silurian carbonate sequences in Europe (Lindström 1884) and North America (Hall 1852; Whiteaves 1895; Northrop 1939; Poulsen 1974) are not similar taxonomically.

TEXT-FIG. 2. Distribution of gastropods within the Arisaig Group. Numbers to the left of species names refer to the morphological groupings employed in the text. 1, high spired. 2, micromorphic high spired. 3, explanate bellerophontacean. 4, micromorphic bellerophontacean. 5, trilobed bellerophontacean. 6, other small bellerophontaceans. 7, lenticular pleurotomariacean. 8, trochiform pleurotomariacean. 9, trochiform murchisoniacean. 10, trochiform platyceratid. 11, trochiform holopeid. 12, other gastropods.


6 undet. bellerophontacean sp. A
6 undet. bellerophontacean sp. B
7 Liospira cf. L. affinis
8 Loxoplocus (Lophospira) sedgwicki
8 L. (Lo.) sp. A
8 L. (Lo.) sp. B
8 Longstaffia sp.
8 Arjamannia cancellatula
8 A. woodlandi
8 Phanerotrema affin. P. jugosum
10 Naticonema kauffmani
10 Cyclonema (C.) parvimedium
12 undet. trochinid sp.
7 Eotomaria sp.
8 Longstaffia centervillensis
12 undet. holopeid sp.
10 Platyceras (P.) cf. Pl. (P.) humilis
7 Umbospira yochelsoni
11 Gyronema haliburtoni
1 Murchisonia (Hormotoma) sp. A
1 Loxonema sp. B
5 Tritonophon sp.
6 Bucanopsis sp.
11 Holopea rossbrookiensis
6 undet. bellerophontacean sp. C
4 Tropidodiscus (?) arisaigensis
8 Arjamannia aulangonensis
6 Cymbularia sp.
5 Plectonotus boucoti
6 Pharetrolites bambachi
1 M. (Sinuspira) cf. M. (S.) tenera
2 Morania (?) sp.
1 Loxonema sp. A
1 Murchisonia (Hormotoma) sp. B
12 Mimospira abbae
5 Tritonophon trilobata
3 Phragmosphaera globata
6 Cymbularia carinata
12 undet. gyronematinid sp.
12 Naticopsis trevorpatriciorum
2 Murchisonia (s.l.) antigonishensis
9 Seelya moydartensis
6 Pharetrolites murchisoni
10 Platyceras (P.) cornutum
undet. high spired gastropods
undet. gastropods
5 Plectonotus cherylae
5 Tritonophon kivitalonae
3 Anapetopsis maclearni
3 A. lalajae
6 undet. bellerophontacean sp. D
12 Onychochilus (?) reversa
7 Liospira marklandensis
8 Brachytomaria sp.
12 Platyconus (?) sp.
12 undet. trochonematid sp.
12 Haplospira sibeliuxeni
10 Cyclonema (C.) lydiamariarum
1 Murchisonia (M.) aciculata
1 M. (M.) amii
1 M. (?Homotoma) arisaigensis
1 Loxonema sinuosum
1 Morania (?) boltoni
12 Auriptygma sp.
BEECHHILL COVE FM.
L.
M.
U.
ROSS BROOK FM.
FRENCH RIVER FM.
DOCTORS BROOK FM.
L.
U.
McADAM BROOK FM.
L.
U.
MOYDART FM.
L.
U.
STONEHOUSE FM.
LLANDOVERY
WENLOCK
LUDLOW
PRIDOLI

Consequently, such widely distributed and well-known Silurian gastropods as the strongly ornamented *Poleumita* and the flange-bearing *Euomphalopterus* have not been recorded from Arisaig, although they may also prove to be characteristic of more offshore assemblages than those preserved in this area (Boucot 1975).

PALAEOENVIRONMENTS OF THE ARISAIG GROUP

Boucot *et al.* (1974) remarked that the Arisaig Group (text-figs. 2, 3) is unique in providing an almost continuous faunal record of a shallow marine environment

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EXPLANATION OF PLATE 27

GSC = Geological Survey of Canada, Ottawa; USNM = U.S. National Museum, Washington D.C.; YPM = Yale Peabody Museum, New Haven.

Fig. 1. *Holopea rossbrookiensis* Peel, 1977. Trochiform holopeid, upper Ross Brook Fm. YPM 28333, holotype, × 2.

Fig. 2. *Platyceras* (*Platyostoma*) *cornutum* (Hisinger, 1837). Coprophagous trochiform platyceratid, lower Moydart Fm. GSC 33272, × 2.

Fig. 3. *Tritonophon kivitalonae* Peel, 1974. Trilobed plectonotinid bellerophontacean, upper Stonehouse Fm. GSC 32782, × 3.

Fig. 4. *Gyronema haliburtoni* (McLearn, 1924). Trochiform holopeid, upper Ross Brook Fm. YPM 462B, holotype, × 3.

Figs. 5, 6. *Anapetopsis maclearni* Peel, 1975*a*. Explanate bellerophontacean, upper Stonehouse Fm. GSC 3140a, holotype, × 2.

Figs. 7, 13. *Liospira marklandensis* McLearn, 1924. Lenticular pleurotomariacean, upper Stonehouse Fm. GSC 5654, holotype, × 2.

Fig. 8. *Tritonophon trilobata* (Sowerby *in* Murchison 1839). Trilobed plectonotinid bellerophontacean, lower Moydart Fm. USNM 169594, × 3.

Fig. 9. *Umbospira yochelsoni* Peel, in press. Lenticular pleurotomariacean, upper Ross Brook Fm. YPM 28330, holotype, × 2.

Fig. 10. *Seelya moydartensis* McLearn, 1924. Trochiform murchisoniacean, lower Moydart Fm. YPM 464A, × 1.

Fig. 11. *Loxonema sinuosum* (Sowerby *in* Murchison 1839). High-spired loxonematacean, upper Stonehouse Fm. YPM 28337A, × 3.

Fig. 12. *Pharetrolites murchisoni* (d'Orbigny, 1848). 'Other' bellerophontacean, lower Moydart Fm. USNM 169461, × 2.

Fig. 14. *Murchisonia* (*M.*) *aciculata* Hall, 1860. High-spired murchisoniid, upper Stonehouse Fm. GSC 5651, × 4.

Fig. 15. *Arjamannia aulangonensis* Peel, 1975*b*. Trochiform pleurotomariacean, Doctors Brook Fm. USNM 169469, holotype, × 2.

Fig. 16. *Morania*(?) *boltoni* Peel, 1975*c*. High-spired loxonematacean, upper Stonehouse Fm. USNM 192120, holotype, × 2.

Figs. 17, 21. *Bucanopsis* sp. 'Other' bellerophontacean, Doctors Brook Fm. USNM 169466, × 2.

Fig. 18. *Longstaffia centervillensis* (Foerste, 1923). Trochiform pleurotomariacean, Beechhill Cove Fm. USNM 188524, × 2.

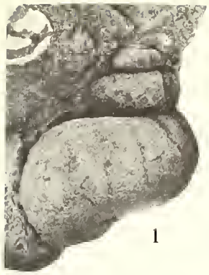
Fig. 19. *Murchisonia* (*M.*) *amii* (McLearn, 1924). High-spired murchisoniid, upper Stonehouse Fm. GSC 5652, holotype, × 3.

Fig. 20. *Plectonotus boucoti* Peel, 1974. Trilobed plectonotinid bellerophontacean, Doctors Brook Fm. USNM 169583, × 5.

Fig. 22. *Loxoplocus* (*Lophospira*) sp. A. Trochiform pleurotomariacean, Beechhill Cove Fm. USNM 169482, × 2.

Fig. 23. *Cyclonema* (*C.*) *parvimedium* McLearn, 1924. Trochiform platyceratid, Beechhill Cove Fm. USNM 169473, × 1.

PLATE 27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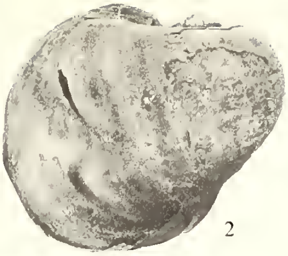
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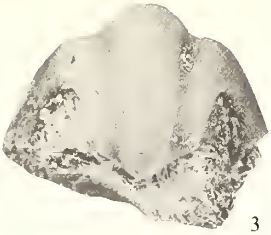
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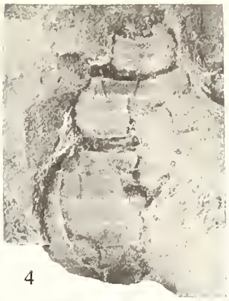
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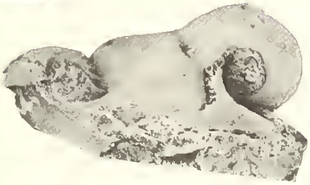
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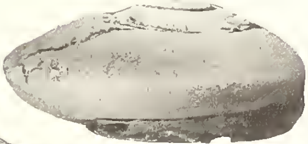
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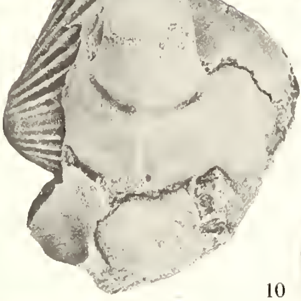
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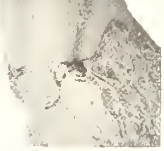
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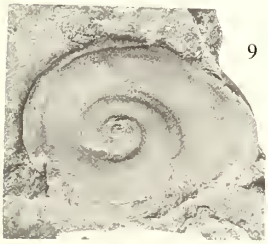
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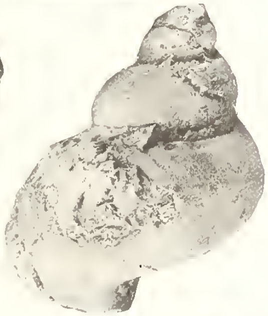
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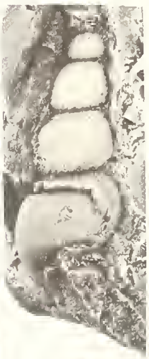
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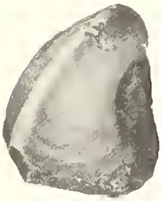
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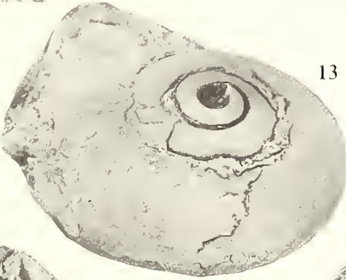
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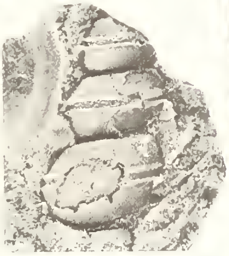
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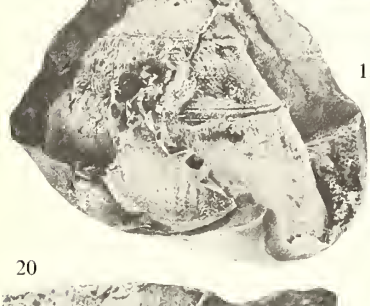
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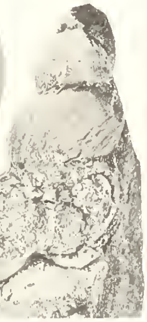
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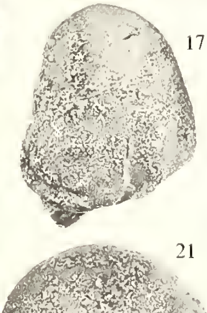
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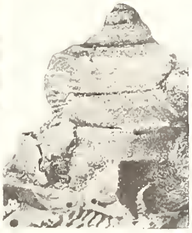
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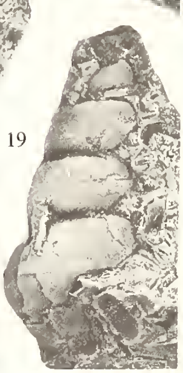
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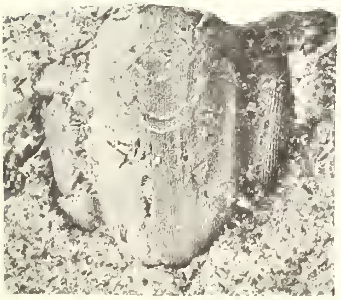
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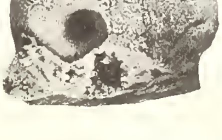
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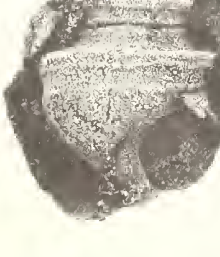
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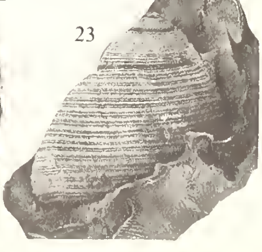
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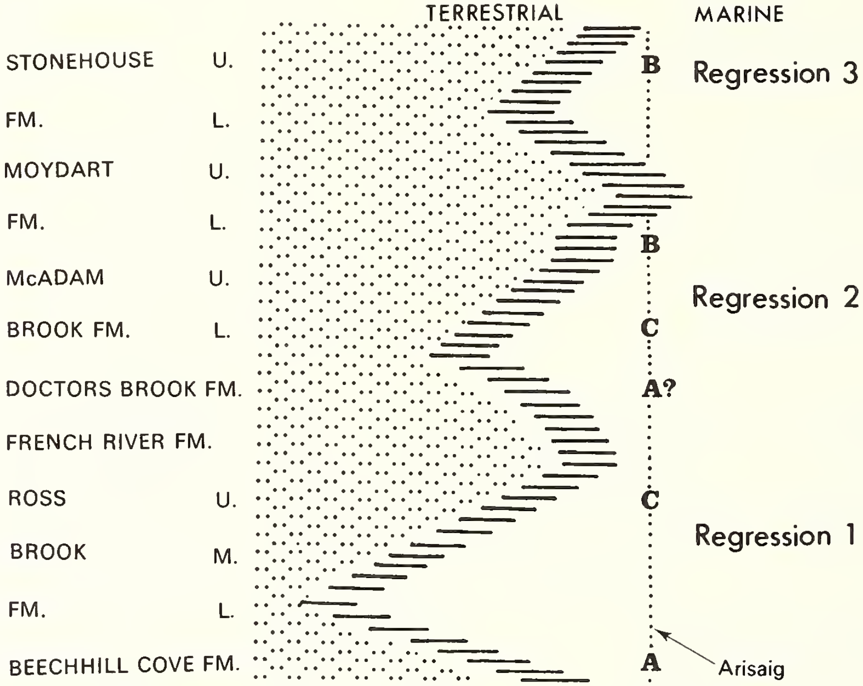
PEEL, Silurian gastropods

throughout the Silurian. Watkins and Boucot (1975) subsequently discussed the succession of brachiopod communities at Arisaig and concluded that most could be referred to the near-shore Benthic Assemblage 2 of Boucot (1975), although the French River Formation has an off-shore Benthic Assemblage 3 or 4 association.

Bambach (1969) presented a sedimentary facies model for the Arisaig Group in the course of an exhaustive study of bivalve palaeoecology. He accepted the general near-shore origin suggested by Boucot *et al.* (1974; in prep. at that time), in which even the deepest part of the succession (represented by the lower Ross Brook Formation) was considered to lie within the *Eocoelia* community of Boucot's Benthic Assemblage 2.



TEXT-FIG. 3. Distribution of gastropod faunas in the three regressive phases of the Arisaig Group. A, hard-bottom, shallow marine platform fauna. B, soft-bottom, shallow marine platform fauna. C, soft-bottom, open lagoon fauna. The vertical broken line represents the approximate position of the Arisaig Group sequence in the simplified facies model (after Bambach 1969).

Bambach recognized three major regressive events during the deposition of the Arisaig Group (text-fig. 3). An initial transgression across underlying non-marine volcanics is represented by the Beechhill Cove Formation. Hard, grey-green quartzose siltstones and thin micaceous shales contain only linguloid brachiopods and crinoid ossicles, but occasional fine sandstone lenses, probably representing storm layers, contain brachiopod-rich basal coquinas.

The Ross Brook and French River formations represent a regressive phase with passage from the deepest water deposits of the Arisaig Group to shoaling barrier deposits in the French River Formation. Fissile graptolitic shales in the lower Ross Brook Formation represent fine muds possibly with an originally high water content. Increased silt content in the middle and upper members of the Ross Brook Formation reflects shallowing and probably produced a stabilized substratum capable of supporting a rich epifauna. Massive siltstones with oolitic ironstone of the French River Formation were considered to represent a barrier bar behind which the shallow-water siltstones of the Doctors Brook Formation were deposited.

A second regressive phase followed an increase in water depth in the earliest McAdam Brook Formation where dark shales comparable to those of the lower Ross Brook Formation occur. Younger strata in the formation contain increasingly higher quantities of silt with massive shoreline siltstones characterizing the succeeding lower Moydart Formation. The regression continued with deposition of non-marine red beds in the upper Moydart Formation.

Massive shoreline siltstones again dominate the lower Stonehouse Formation, but are followed by open marine platform shales, siltstones, and thin limestones in the upper member. A third regression, producing a gradual shallowing in the later part of the upper Stonehouse Formation, culminates in a return to non-marine red bed deposition in the Devonian Knoydart Formation.

GASTROPOD FAUNAL TYPES

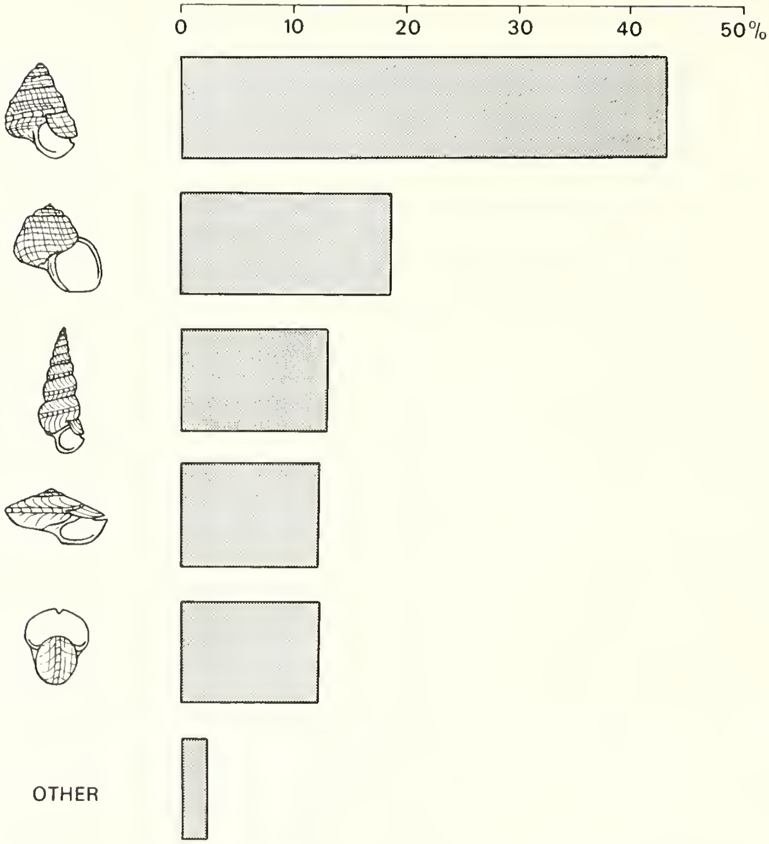
Three associations of gastropods are recognized in the Arisaig Group on the basis of their principal constituent morphological groups and partial recurrence in the sedimentary model of Bambach (1969). Interpretation of modes of life of gastropods within the morphological groups, which add further support to the delimitation of faunal types, is attempted in a later section.

Hard-bottom, shallow marine platform fauna. This fauna is characterized by a dominance of large (up to 25 mm) trochiform pleurotomariaceans, both in terms of individuals and number of species. Trochiform holopeids, explanate bellerophontaceans, and trochiform murchisoniaceans, interpreted below as associated with a soft bottom, are absent. High-spired gastropods are present, but not dominant as in the soft-bottom, shallow marine platform fauna.

The fauna is typically developed in the transgressive Beechhill Cove Formation (text-figs. 2, 4) where the large (20–30 mm) trochiform platyceratacean *Cyclonema* (*C.*) *parvimedium* is also conspicuous. Lenticular pleurotomariaceans and the globose bellerophontacean *Bucanopsis* sp. (Pl. 27, figs. 17, 21) are also well represented, but not considered diagnostic.

The hard-bottom, shallow marine platform fauna may also be represented in the Doctors Brook Formation (text-figs. 2, 3), although trochiform pleurotomariaceans are rare, and trilobed plectonotinid bellerophontaceans are dominant. This may suggest more shallow-water or near-shore conditions than in the Beechhill Cove Formation, where only a single plectonotinid is recorded (see discussion below).

Soft-bottom, shallow marine platform fauna. The soft-bottom, shallow marine platform fauna is dominated by high-spired murchisoniids and loxonemataceans, associated

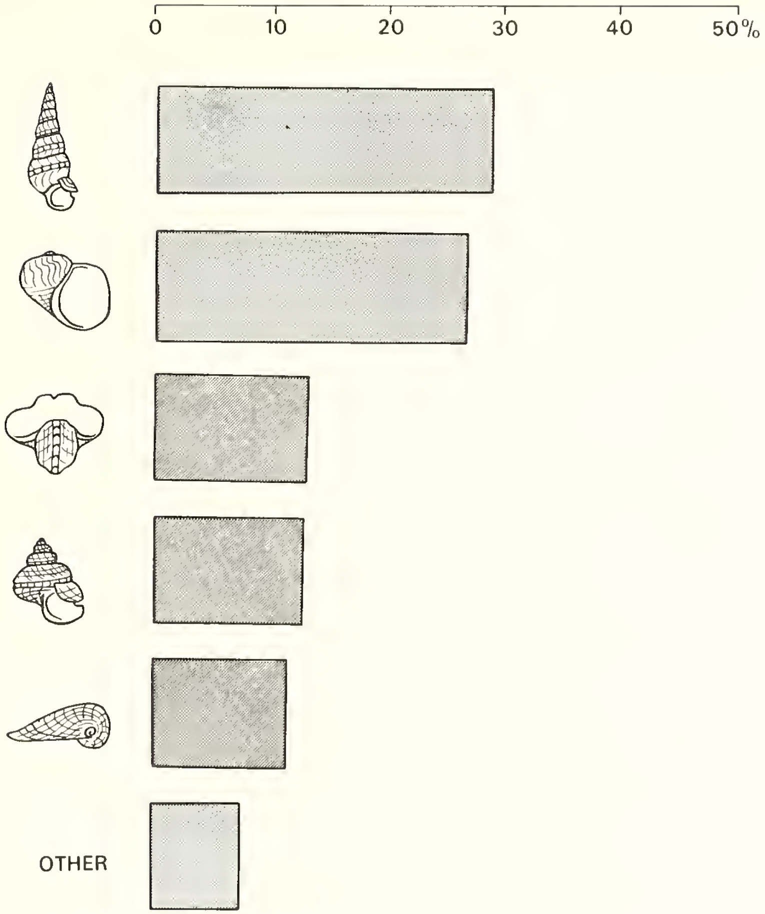


TEXT-FIG. 4. Composition of hard-bottom, shallow marine platform fauna, Beechhill Cove Formation. In descending order: trochiform pleurotomariaceans, the trochiform platyceratid *Cyclonema* (*C.*) *parvimedium*, high-spired gastropods, lenticular pleurotomariaceans, the small bellerophontacean *Bucanopsis* sp., other gastropods. Total of 146 specimens.

with explanate bellerophontaceans and trochiform murchisoniaceans. Trochiform pleurotomariaceans are almost totally absent, in agreement with the interpreted soft bottom.

Trilobed plectonotinid bellerophontaceans are common, but this abundance is primarily equated with proximity to shore rather than the nature of the sea bottom. Trilobed bellerophontaceans are also well represented in the possible near-shore equivalent of the hard-bottom, shallow marine platform fauna preserved in the Doctors Brook Formation, above, and in the soft-bottom open lagoon fauna described below.

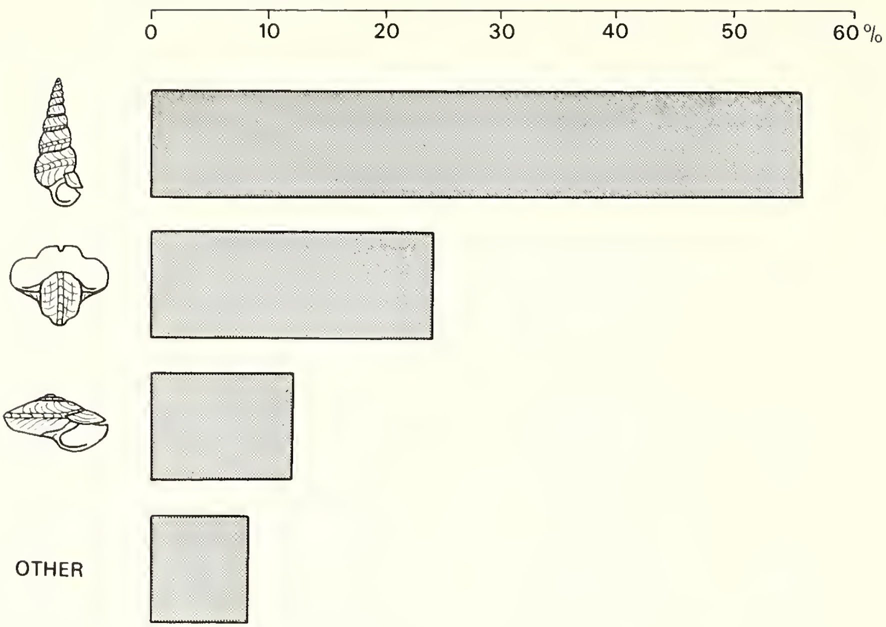
The soft-bottom, shallow marine platform fauna is well represented in the upper Stonehouse Formation and, in a more diverse form, in the lower Moydart Formation (text-figs. 2, 5, 6), the latter during a brief lull in massive shore-line siltstone deposition. In the Stonehouse Formation the lenticular pleurotomariacean *Liospira marklandensis*



TEXT-FIG. 5. Composition of soft-bottom, shallow marine platform fauna, lower Moydart Formation. In descending order: high-spired gastropods, the trochiform platyceratid *Platyceras* (*Platyostoma*) *cornutum*, trilobed bellerophontacean *Tritonophon trilobata*, trochiform murchisoniacean *Seelya moydartensis*, explanate bellerophontacean *Phragmosphaera globata*, other gastropods. Total of 159 specimens.

(Pl. 27, figs. 7, 13) is common, and the explanate bellerophontacean *Anapetopsis* (Pl. 27, figs. 5, 6) somewhat infrequent. In the Moydart Formation, the trochiform murchisoniaceans *Seelya moydartensis* and explanate bellerophontacean *Phragmosphaera globata* are common additional elements. Abundant coprophagous platyceratids reflect the presence of the best preserved crinoid remains in the Arisaig Group, but are not considered definitive of fauna B.

Soft-bottom, open-lagoon fauna. In its typical development in the lower beds of the upper Ross Brook Formation, this fauna is heavily dominated by the trochiform holopeids *Gyronema* and *Holopea* (Pl. 27, figs. 1, 4). With a decrease in water depth the holopeids are replaced by a fauna of small bellerophontaceans, including trilobed plectonotinids,



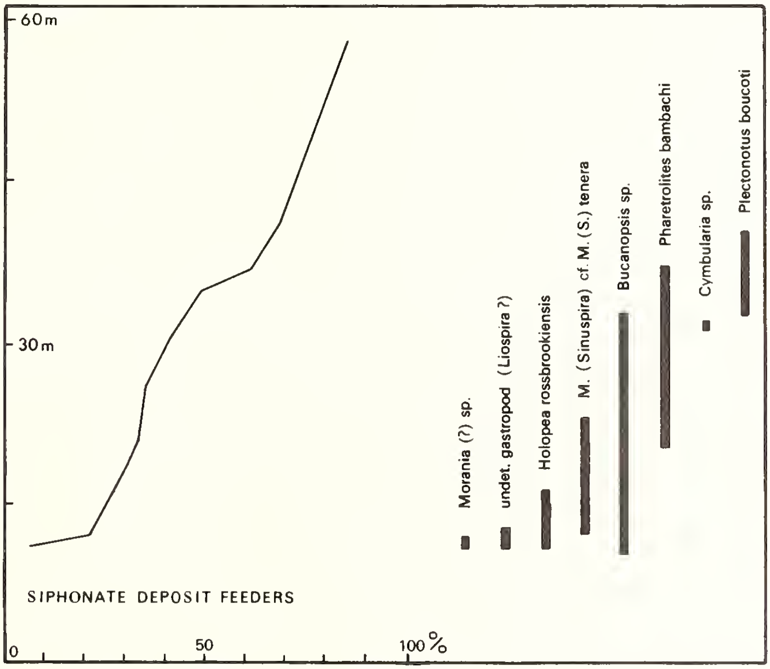
TEXT-FIG. 6. Composition of soft-bottom, shallow marine platform fauna, upper Stonehouse Formation. In descending order: high-spired gastropods, trilobed bellerophontaceans, the lenticular pleurotomariacean *Liospira marklandensis*, other gastropods. Total of 353 specimens.

associated with lenticular pleurotomariaceans and some high-spired gastropods. This shallower-water equivalent of the typical soft-bottom, open-lagoon fauna also lacks the abundant trochiform pleurotomariaceans characteristic of the hard-bottom, shallow marine platform fauna, or the over-all dominance by high-spired gastropods typical of the soft-bottom, shallow marine platform fauna.

The soft-bottom, open-lagoon fauna is also preserved in the lower McAdam Brook Formation, although the typical holopeids are more restricted and soon give way to the more shallow-water elements. Here, a parallel change has been documented by Levinton and Bambach (1975) in the composition of bivalve faunas. Deposit feeding bivalves dominate throughout, but non-siphonate forms are gradually replaced by siphonate species in a change which Levinton and Bambach related to increasing firmness of the later, more near-shore deposits (text-fig. 7).

Comparable faunas from other areas. The parallel development of gastropod faunas respectively dominated by trochiform pleurotomariaceans and high-spired gastropods, i.e. the hard-bottom, and soft-bottom, shallow marine platform faunas as reported above, has been described by Bretsky (1970) from the upper Ordovician of the central Appalachians. Lophospirid, trochiform pleurotomariaceans occur in a *Sowerbyella-Onniella* Community developed on outer sublittoral sands, while high-spired murchisoniids are the characteristic gastropods in an inner to outer sublittoral *Zygospira-Hebertella* Community developed on calcareous muds.

An antipathetic relationship between trilobed plectonotinid bellerophontaceans and the trochiform holopeid '*Gyronema* cf. *octavia*' described by Shaw (1971) from the upper Silurian of the English Lake District may represent the passage from a soft-bottom, open-lagoon fauna as interpreted here, to its near-shore equivalent with small bellerophontaceans. Shaw maintained that the holopeid dominated in more stable areas of slow sedimentation, while the plectonotinid was typical of more rapidly sedimented, perhaps deeper-water areas. Shaw's conclusions with regard to depth are in apparent contradiction with the evidence from Arisaig, where plectonotinids are attributed a more near-shore life habit than trochiform holopeids. However, the presence of holopeids in the fine-grained sediments of the Ross Brook Formation may be in agreement with Shaw's observation concerning slow sedimentation. Similarly, the presence of trilobed plectonotinids higher in the inferred shallowing sequence, interbedded with shoal-deposited siltstones, may equally explain Shaw's claim for more unstable conditions.



TEXT-FIG. 7. Distribution of siphonate deposit-feeding bivalves, and gastropods in the lower McAdam Brook Formation. Increase in siphonate deposit feeders ascribed to increasing firmness of progressively more near-shore deposits parallels a gradual change in the gastropod fauna from elements of the soft-bottom, open lagoon fauna to more shallow-water equivalents. Bivalve and section data compiled after Bambach (1969) and Levinton and Bambach (1975). Total of 54 gastropods.

GASTROPOD FAUNAL SUCCESSION

The three generalized gastropod faunas described above are partially repeated in the Arisaig Group (text-fig. 3) as a result of the repetition of environments in the three regressive phases described by Bambach (1969). The repetition, which is particularly evident in the case of the two soft-bottom associations, serves to emphasize the integrity of the faunal division based on morphological groups, since very few species survive from one regressive phase to the next (text-fig. 2). However, morphologically equivalent species can be recognized in successive phases, and the gross morphological composition of the respective faunas is largely unchanged.

The hard-bottom, shallow marine platform fauna is developed in the transgressive Beechhill Cove Formation (fauna A in text-fig. 3) and succeeded by a soft-bottom, open lagoon fauna during the first regressive phase (fauna C). The few gastropods known from the French River Formation are too meagre to evaluate, but the hard-bottom fauna possibly reoccurs in the Doctors Brook Formation with rare specimens of a different species of the trochiform pleurotomariacean *Arjamannia* than those known from the Beechhill Cove Formation (text-figs. 2, 3).

The soft-bottom, open lagoon fauna is again evident in the second regressive phase, with *Holopea rossbrookiensis* reappearing in the McAdam Brook Formation after its initial occurrence in the Ross Brook Formation. *Bucanopsis* sp. also reappears, but new species of trilobed plectonotinids and high-spired gastropods are found. The reduced representation of holopeids in the second regressive phase may suggest somewhat more near-shore conditions initially, relative to the first regressive phase, which is in accordance with Bambach's (1969) proposal that the lower Ross Brook Formation contains the deepest-water deposits within the Arisaig Group.

Later in the second regressive phase, the soft-bottom, shallow marine platform fauna occurs in the lower Moydart Formation (fauna B in text-fig. 3) prior to non-marine red-bed deposition in the upper Moydart Formation.

Sufficiently off-shore conditions suitable for the establishment of the open-lagoon fauna were not developed in the third sedimentary cycle. The soft-bottom, shallow marine platform fauna is, however, well represented in the upper Stonehouse Formation (B in text-fig. 3) before red-bed deposition once more returned in the overlying Knoydart Formation (Devonian). *Pharetrolites murchisoni* and the ubiquitous *Platyceras* (*Platyostoma*) *cornutum* reappear in the upper Stonehouse Formation, after being present in the previous regressive phase, but the morphologically similar faunas do not otherwise have species in common.

MODE OF LIFE OF LOWER PALAEOZOIC GASTROPODS

All the Arisaig gastropods listed in text-fig. 2, with the exception of six species assigned to the caenogastropods *Loxonema*, *Morania*(?), and *Auriptygma*, were placed within the Order Archaeogastropoda by Knight *et al.* (1960). Recent members of the order are herbivores, which are generally restricted to a harder bottom in conditions of clear water, since their bipectinate ctenidia cannot satisfactorily cope with fine, suspended sediment (Yonge 1947). In contrast, living members of the Caenogastropoda (= Mesogastropoda + Neogastropoda), which now comprise two-thirds of the prosobranch gastropod fauna of recent seas, have a monopectinate ctenidium enabling free movement into environments characterized by soft sediment.

The rise to dominance of caenogastropods since the Lower Palaeozoic has possibly resulted in a parallel diminution in the range of habitats occupied by archaeogastropods. Recent archaeogastropods may therefore have a narrower environmental range than their Palaeozoic ancestors, due to competition with the increasingly abundant caenogastropods. Thus, Lower Palaeozoic archaeogastropods should not *automatically* be interpreted as herbivores limited to hard bottoms in clear water in similar fashion to most of their extant descendants.

Some non-herbivores are already known in the Lower Palaeozoic—many platyceratids lived on the calyx of echinoderms and ingested expelled faeces (Bowsher 1955). Related platyceratids may easily have been benthic scavengers. True carnivorous gastropods have not been certainly recognized, although it is quite possible that some Palaeozoic gastropods fed on sponges in similar fashion to some extant 'primitive' archaeogastropods of the family Fissurellidae (Morton 1967).

Similarly, other Palaeozoic gastropods may be common in fine sediments seemingly indicative of a soft bottom (Foerste 1923; Craig 1954; Wilson 1966; Bretsky 1970). In some cases, as for example in the fauna of small Carboniferous gastropods from Poland described by Gromczakiewicz-Lomnicka (1972), the occurrence of gastropods can be satisfactorily interpreted in relation to life amongst algal foliage, high above the possibly turbid sediment/water interface. In other cases, unusual shell morphologies are readily interpreted as adaptations to life on a soft bottom. Thus, Peel (1975*a*) proposed that the widely expanded, explanate aperture of the Arisaig bellerophontacean *Anapetopsis* (Pl. 27, figs. 5, 6) was an adaptation to a soft bottom. A more generally significant example, the correlation between the high-spired shell form and low-energy environments (including infaunal) by Vermeij (1971), is more fully discussed below.

Determination of the former life habits of Lower Palaeozoic gastropods must depend heavily on the establishment of parallels between present-day and fossil morphological adaptations. Unfortunately, the average trochiform gastropod shell can be found in most present-day environments. In addition, widely different ranges of shell morphologies are present in Recent and Palaeozoic gastropod faunas as a result of evolutionary changes in faunal composition (Vermeij 1975). There are also dangers associated with such morphological comparisons, as can be readily seen from comparing the Recent pleurotomariids *Perotrochus*, *Mikadotrochus*, and *Entemnotrochus* with their very close morphological analogues from the Palaeozoic. The Recent species are restricted to deeper water, while the more abundant Palaeozoic species are demonstrably shallow-water dwellers. However, favourable parallels can often be established for more unusual morphologies. Thus, the soft-bottom mode of life inferred above for the explanate bellerophontacean *Anapetopsis* on morphological grounds, is supported by comparison with the present-day pelican's foot shells *Aporrhais pespelicani* and *A. serresiana* (Yonge 1937). Hyperstrophic, open coiling in the soft-bottom dwelling *Nevadaspira* from the Devonian led Yochelson (1971) to suggest a sedentary, ciliary feeding mode of life. Peel (1975*d*) suggested a similar existence for other Palaeozoic uncoiled and open-coiled gastropods, including forms resembling *Vermicularia*.

LIFE HABITS OF ARISAIG GASTROPODS

Different gastropod morphotypes in the Arisaig Group can be loosely assigned to three main life habits—soft-bottom dwellers, hard-bottom dwellers, and foliage dwellers—although some shell morphologies may occur in all three, e.g. high-spired gastropods. Assignment of individual morphological groups to trophic units is often unsatisfactory, since several groups contain gastropods that probably employed different methods of food gathering. Present-day high-spired gastropods, for example, may be ciliary feeders (*Turritella*), grazing herbivores, or deposit feeders (cerithiids), foliage dwellers (*Bittium*), or active infaunal predators (terebrids). However, all share certain common adaptive shell features which can be recognized in analogous Palaeozoic lineages. In this case, the possible feeding patterns of the Palaeozoic high-spired gastropods must then be deduced from evidence other than the basic shell morphology.

SOFT-BOTTOM DWELLING GASTROPODS

High-spired gastropods. High-spired murchisoniids and loxonematacean gastropods (Pl. 27, figs. 11, 14, 16, 19) are frequently abundant in assemblages from the Arisaig Group (text-fig. 2, species of *Murchisonia*, *Loxonema*, and *Morania*(?)). They form the dominant element in the soft-bottom, shallow marine platform fauna (text-figs. 5, 6), but may also be well represented in the hard-bottom, shallow marine platform fauna (text-fig. 4) and, to a lesser extent in the soft-bottom, open lagoon fauna.

The inability of the bipectinate ctenidia of Recent archaeogastropods to cope satisfactorily with fine, suspended sediment generally restricts members of the Order Archaeogastropoda to a firm bottom in conditions of clear water (Yonge 1947). Vermeij (1971) argued that the absence of the high-spired shell form amongst Recent archaeogastropods probably resulted from this restriction, since a high-spired shell is not physically stable in the higher-energy conditions associated with a hard bottom. The high-spired shell form is advantageous only in low-energy environments, or infaunally. The general equivalence of soft sediments and sea bottom with low-energy environments therefore tends to limit the high-spired shell form to the monopectinate caenogastropods, since archaeogastropod bipectinate ctenidia are unsuited to the turbid conditions in such an environment.

Loxonemataceans were considered to be caenogastropods by Knight *et al.* (1960) and, as such, probably moved freely in soft sediments. Murchisoniids, the most common Lower Palaeozoic high-spired gastropods, were only tentatively assigned to the Archaeogastropoda by Knight *et al.* (1960), since they combine the well-developed slit and selenizone characteristic of the Pleurotomariina and Bellerophontina with the high-spired form and other features of the Caenogastropoda.

Vermeij's (1971) stability arguments suggest that murchisoniids generally lived on a soft bottom in low-energy environments. Indeed, they may be common in fine sediments seemingly indicative of such conditions (Foerste 1923; Bretsky 1970). Consequently, murchisoniids are probably best interpreted as monopectinate caenogastropods, as also suggested by Bretsky (1970), although some form of modified bipectinate ctenidia unknown in extant archaeogastropods may have been present.

It must be remembered, however, that some Palaeozoic archaeogastropods, e.g. explanate bellerophontaceans, were apparently able to move freely over soft sediments. An alternative to the caenogastropod (or modified archaeogastropod) interpretation could be that murchisoniids were archaeogastropods with relatively normal bipectinate ctenidia, and that the post-Palaeozoic rise to dominance of caenogastropods with a more efficient monopectinate ctenidium may now effectively deny this environment to the less-efficient bipectinate archaeogastropods.

Some Lower Palaeozoic high-spired gastropods may have been ciliary feeders comparable to the present-day *Turritella* (Peel 1975*d*; 1977), scavengers, or even sluggish carnivores, on sedentary organisms in similar fashion to Recent epitoniids (Keen 1971; Morton and Miller 1973). However, most probably lived in a comparable way to extant herbivorous cerithiids. Many are microherbivores living on the algal-coated surfaces of fine sediments (Taylor 1971), as may have the murchisoniids and loxonematids dominating the soft-bottom, shallow marine platform fauna. Others live infaunally in sand (Keen 1971), which may partly explain the relatively large proportion of high-spired gastropods present in the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation (text-fig. 4). Other tiny species live amongst algal foliage (e.g. *Bittium*; Duffus 1969) and this mode of life can also be suggested for two small (less than 10 mm) Arisaig species—*Murchisonia s.l. antigonishensis* from the lower Moydart Formation, and *Morania*(?) sp. from the McAdam Brook Formation.

Explanate bellerophontaceans. Many unrelated bellerophontacean genera greatly increase the rate of whorl expansion in the final growth stage, so that the margins of the aperture become tangential to the substratum, i.e. explanate. Peel (1975*a*), in describing the explanate *Anapetopsis* (Pl. 27, figs. 5, 6) from the Stonehouse Formation at Arisaig, suggested that this morphology was an adaptation to life on a soft bottom. Enlargement of the gastropod foot associated with the expansion of the shell may have helped prevent submergence of the gastropod into soft sediment and could have lowered the amount of sediment raised into suspension by the gastropod's movements.

Phragmosphaera globata from the lower Moydart Formation is less bell-shaped than *Anapetopsis*, and has less finely tapering shell margins. It is possible that *P. globata* lived on a slightly harder bottom than *Anapetopsis*, by analogy with the present-day pelican's foot shell *Aporrhais*. The deeper water, soft-sediment dwelling *Ap. serresiana* has longer, more delicate digitations than occur in *Ap. pespelicani*, a thicker-shelled, muddy-sand dweller (Yonge 1937).

Explanate bellerophontaceans are characteristic of the soft-bottom, shallow marine platform fauna at Arisaig. *P. globata* is common in the lower Moydart Formation, while two species of *Anapetopsis* occur more rarely in the upper Stonehouse Formation (text-fig. 2).

A comparable relationship between explanate bellerophontaceans and a soft bottom has been described by Gromczakiewicz-Lomnicka (1972) from the Carboniferous of Poland. The bellerophontacean *Patellilabia*, a homeomorph of *Anapetopsis*, is the only large gastropod in a fauna of otherwise diminutive, algal-foliage dwelling gastropods in a black shale.

Trochiform murchisoniacean. The trochiform murchisoniacean *Seelya moydartensis* (Pl. 27, fig. 10) closely resembles members of the trochiform pleurotomariacean group characteristic of the hard-bottom, shallow marine platform fauna. However, the presence of an incipient anterior siphonal notch led Knight *et al.* (1960) to refer *Seelya* to the Murchisoniina, as a relative of the high-spired murchisoniids. The implied ability to move freely on soft sediment inherent in this systematic position, now that the Murchisoniina are considered to be caenogastropods or their functional equivalents, is substantiated by the Arisaig occurrence where *S. moydartensis* is associated with abundant high-spired gastropods and explanate bellerophontaceans in the soft-bottom, shallow marine platform fauna of the lower Moydart Formation.

Trochiform holopeids. Gyronema haliburtoni (Pl. 27, fig. 4) and *Holopea rossbrookiensis* (Pl. 27, fig. 1), the diagnostic element of the soft-bottom, open lagoon fauna are common in shales and mudstones in the lower part of the upper member of the Ross Brook Formation (text-fig. 2), which probably represent an originally soft bottom. The supposed bipectinate ctenidia of holopeids classically argues against life in such an environment, but this appears to be in conflict with the sedimentological evidence. It is possible that the holopeids were archaeogastropods adapted to soft sediment, or even that their affinities lie with the Caenogastropoda rather than with the Archaeogastropoda. Alternatively, holopeids may have lived amongst algal foliage in comparable fashion to members of a present-day trochid association in *Zostera* meadows noted by Morton and Miller (1973) in New Zealand. However, the Arisaig holopeids (up to 30 mm high) are relatively much larger than most of the trochids in the present-day association.

Trilobed plectonotinid bellerophontaceans are considered to be foliage dwellers, although their almost total absence (one recorded specimen) from the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation may indicate some correlation with a soft bottom. An alternative hypothesis involving a more off-shore origin for the Beechhill Cove Formation fauna than was suited to plectonotinids is discussed below.

HARD-BOTTOM-DWELLING GASTROPODS

The characteristic gastropods of the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation are trochiform pleurotomariaceans and certain trochiform platyceratids. A variety of other gastropods may also be present (text-figs. 2, 4) but are not considered to be diagnostic. Of particular note amongst these is the relative prominence of high-spired gastropods which characteristically dominate the soft-bottom, shallow marine platform fauna. The Beechhill Cove Formation high-spired gastropods are generally too poorly preserved for determination even to family, and therefore cannot be closely compared to forms in the rest of the Arisaig sequence. However, many probably lived infaunally, as do some recent cerithiids (Keen 1971), so that the low-stability shell (Vermeij 1971) was not exposed to the higher-energy environment at and above the surface of the sediment.

Trochiform pleurotomariaceans of the genera *Arjamannia* (Pl. 27, fig. 15), *Longstaffia* (Pl. 27, fig. 18), *Loxoplocus* (*Lophospira*) (Pl. 27, fig. 22), and *Phanerotrema* are common in the Beechhill Cove Formation (text-figs. 1, 4) and form the diagnostic elements of the hard-bottom, shallow marine platform fauna. The rare Recent pleurotomariids *Entemnotrochus*, *Mikadotrochus*, and *Perotrochus* are morphologically very close to these extinct Palaeozoic genera, but are restricted to deep water (Batten 1958) in conditions quite unlike the shallow water, near-shore environment envisaged during the deposition of the Arisaig Group.

The presence of bipectinate ctenidia would be expected to limit trochiform pleurotomariaceans to a firm bottom in clear water (Yonge 1947), and this pattern is supported by their distribution at Arisaig. Many of the pleurotomariaceans reach a height in excess of 25 mm, suggesting life as epifaunal deposit feeders.

Trochiform platyceratids. The coprophagous habit of some platyceratids on echinoderms is well known (Bowsher 1955). Irregularities in the apertural margin of the gastropod (Pl. 27, fig. 2) commonly correspond to the shape of the surface of the echinoderm calyx. However, other platyceratids (e.g. *Cyclonema* (*C.*) *parvimedium*, Beechhill Cove Formation; Pl. 27, fig. 23) have more regular growth lines and ornamentation and were probably benthic scavengers or sluggish carnivores on sedentary organisms. Large (20–30 mm) specimens of *C.* (*C.*) *parvimedium* are typical of the hard-bottom, shallow marine platform fauna in the Beechhill Cove Formation. The genus is otherwise known at Arisaig only from a single poorly preserved specimen of *C.* (*C.*) *lydiamariarum* in the upper Stonehouse Formation (Peel 1975*c*).

ALGAL-FOLIAGE SUPPORTED GASTROPODS

In Recent assemblages abundant gastropods live among the foliage of marine algae and sea-grasses. The plants provide a protective habitat with abundant food above a possibly turbid sediment/water interface. Foliage-supported faunas are often well stratified, with distinctive suites of species living at the sediment surface, amongst the holdfasts or roots, and at various levels within the foliage (Morton and Miller 1973; Starmühlner 1969; Taylor and Lewis 1970). Stratification of faunas in algal foliage provides a possible explanation for the occurrence of archaeogastropods with ctenidia unsuited to turbid water in soft sediments, since undisturbed shell accumulations in such areas may include representatives from the pelagic realm, from any stratum within the foliage, from the sediment surface, or from the infauna.

The molluscs living on seaweed are generally small. Indeed, Brazier (1975) commented that an abundance of small gastropods may be one criterion for the recognition of former grass beds. Warmke and Almodovar (1963) studied the relationship between marine molluscs and algae in Puerto Rico and noted that gastropods comprised 99% of the molluscs in their samples. The vast majority of these were less than 2 mm in length.

Micromorphic gastropods are widely reported in the Palaeozoic (e.g. Gromczakiewicz-Lomnicka 1972; Harrison and Harrison 1975) but, especially in the Lower Palaeozoic, are often poorly preserved and systematically neglected. Most named and described Palaeozoic gastropods are significantly larger than most present-day foliage-supported species. Consequently, a general statement that many of these Palaeozoic gastropods were foliage dwellers is difficult to accept. Only one known

Arisaig gastropod species, *Tropidodiscus*(?) *arisaigensis* from the Doctors Brook Formation, falls within the 2-mm size parameter quoted by Warmke and Almodovar (1963), although this is undoubtedly a partial consequence of preservational and collecting bias.

Many smaller (*c*. 5 mm) Arisaig gastropods (e.g. *Cymbularia carinata*, *Naticopsis trevorpatriciorum*, *Murchisonia* (*s.l.*) *antigonishensis*, *Pharetrolites murchisoni* from the lower Moydart Formation) may also have been foliage dwellers, together with some gastropods reaching twice or three times this size. However, it is difficult to propose that a high proportion of Arisaig gastropods consistently attaining a size of 20 mm or more lived in this manner, although foliage support still provides an attractive interpretation of mode of life for a number of forms of this size discussed below.

The importance of size as a parameter distinct from morphology in evaluation of mode of life is clearly illustrated by comparing trochiform pleurotomariaceans from the Beechhill Cove Formation at Arisaig with their occurrence in the Carboniferous fauna described by Gromczakiewicz-Lomnicka (1972). The two groups of species are morphologically very close, but the epifaunal, deposit-feeding Arisaig specimens are commonly 20–25 mm high—some four or five times as large as the foliage-dwelling Carboniferous species. This size difference is paralleled within high-spired gastropods at Arisaig.

Micromorphic bellerophontacean. The minute, laterally compressed bellerophontacean *Tropidodiscus*(?) *arisaigensis* (length 2 mm), currently known at Arisaig only from the Doctors Brook Formation, was interpreted as a micromorphic adult by Peel (1977) and not as a juvenile of some otherwise unrecognized species. *T.*(?) *arisaigensis* is of comparable size to most Recent gastropods living amongst algal foliage (Warmke and Almodovar 1963; Morton and Miller 1973) and is one of the very few Arisaig species that can be interpreted confidently as having this mode of life.

Micromorphic high-spired gastropods. As noted above, *Murchisonia* (*s.l.*) *antigonishensis* from the lower Moydart Formation, and *Morania*(?) sp. from the McAdam Brook Formation may have lived amongst algal foliage in similar fashion to present-day cerithiids of the same size (Duffus 1969).

Trilobed bellerophontaceans. Peel (1974) discussed the functional morphology and systematics of the trilobed plectonotinid bellerophontaceans *Plectonotus* and *Tritonophon* (Pl. 27, figs. 3, 8, 20) and concluded that trilobation increased the efficiency of the mantle cavity by separating the inhalant and exhalant respiratory currents. As a result of the generally accepted presence of bipectinate ctenidia, trilobed plectonotinids would be expected to favour a firm bottom in clear water, or to be foliage dwellers. The latter seems to be most likely since plectonotiniids, although often 10–15 mm in length, are commonly preserved in fine sediments probably indicative of a rather soft bottom. Bretsky (1970) suggested that a *Plectonotus*(?) sp. in the upper Ordovician of the central Appalachians browsed on algal fronds growing on the silty muds of extremely near-shore lagoons.

Plectonotinids appear to be associated with extreme near-shore conditions. Boucot *et al.* (1969) described a homalonotid-*Plectonotus* Community from the Silurian and Devonian to the landward of Ziegler's *Eocoelia* Community. Bretsky (1970) found them to be characteristic of the most inshore, linguloid, population of his *Orthorhynchula-Ambonychia* Community. At Arisaig, plectonotinids are especially common in the soft-bottom, shallow marine platform faunas of the lower Moydart and upper Stonehouse formations, and in the shallow, shoaling deposits of Doctors Brook Formation. They occur more sparsely in the higher beds of the Ross Brook and McAdam Brook formations as a more near-shore equivalent of the trochiform, holopeid dominated soft-bottom, open-lagoon fauna. Plectonotinids are rare in the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation, where the abundance of *Bucanopsis* sp. may indicate slightly more off-shore conditions than were favourable to plectonotinids (see next section). Alternatively, their virtual absence from the Beechhill Cove Formation could reflect a preference for a softer bottom.

Other bellerophontaceans. A number of other small bellerophontaceans were probably grazers amongst algal foliage in similar fashion to trilobed plectonotinids. This foliage-supported mode of life is especially probable in the lower Moydart Formation, where *Pharetrolites murchisoni* and *Cymbularia carinata* are associated with abundant *Tritonophon trilobata* and other small gastropods (*Naticopsis trevorpatriciorum*, *Murchisonia s.l. antigonishensis*).

Bucanopsis sp. (Pl. 27, figs. 17, 21) is associated with trochiform holopeids in the shallowing cycles of the upper Ross Brook and McAdam Brook formations (text-fig. 2) prior to the incoming of trilobed plectonotinids. This separation of bellerophontaceans may suggest a preference by *Bucanopsis* sp. for slightly more off-shore conditions than those favoured by trilobed plectonotinids. The relative abundance of *Bucanopsis* sp. and the absence of plectonotinids in the Beechhill Cove Formation may suggest that the fauna of the latter lived under more off-shore conditions than the faunas of the lower Moydart and upper Stonehouse formations, where plectonotinids are common.

Lenticular pleurotomariaceans (*Liospira* cf. *L. affinis*, Beechhill Cove Formation; *L. marklandensis*, upper Stonehouse Formation, Pl. 27, figs. 7, 13; *Umbospira yochelsoni*, upper Ross Brook Formation, Pl. 27, fig. 9) have nearly planispiral shells, up to 25 mm in diameter, of similar morphology to laterally compressed bellerophontaceans. An epifaunal deposit-feeding, or foliage-browsing, mode of life is probable. Abundance of lenticular elements may be correlated with shallow water (e.g. compare the well-known *Turbocheilus* [*Platyschisma*] *helicites* beds associated with the transition from marine to non-marine strata in the Silurian of the Welsh Borderlands, the *Platyschisma* community of Boucot 1975). As such, they are abundant in both the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation and the soft-bottom, shallow marine platform fauna of the upper Stonehouse Formation. Their absence from the soft-bottom, shallow marine platform fauna of the lower Moydart Formation is unexplained, although a variety of small foliage-dwelling gastropods is present and may occupy that niche.

Other gastropods. Several small gastropod species are too rare at Arisaig to integrate into the above scheme, although a number were possibly foliage dwellers. This rarity may itself suggest that some of the species, e.g. the caenogastropod *Auriptygma* from the upper Stonehouse Formation, were carnivores (Boucot 1975), although supporting evidence is not available.

The two hyperstrophic species *Onychochilus*(?) *reversa* and *Mimospira abbae*, and the globose *Naticopsis trevorpatriciorum*, all between 5 and 10 mm high, were possibly foliage dwellers.

Three holopeid species (*Haplospira sibeliuxeni*, an undetermined holopeid and an undetermined gyronematinid) were probably members of the trochiform holopeid group discussed above. *Platyconus*(?) sp. and an undetermined trochonematid from the upper Stonehouse Formation, and an undetermined trochinid from the Beechhill Cove Formation, were probably epifaunal deposit feeders.

SUMMARY

Three basic types of gastropod fauna in the Arisaig Group of Nova Scotia are partially repeated in successive regressive phases of sedimentation (text-fig. 3). The morphological composition of the individual repeated faunas is largely unaltered, although taxonomic similarity between successive regressions is low (text-fig. 2).

A hard-bottom, shallow marine platform fauna is dominated by epifaunal, deposit-feeding trochiform pleurotomariaceans and benthic scavengers (*Cyclonema* (*C.*) *parvimedium*). Infaunal, high-spired gastropods, and foliage-dwelling lenticular pleurotomariaceans and small bellerophontaceans (*Bucanopsis* sp.) are well represented.

A soft-bottom, shallow marine platform fauna is characterized by abundant epifaunal, deposit-feeding, high-spired murchisoniids and loxonemataceans. Associated elements include epifaunal deposit-feeding explanate bellerophontaceans and trochiform murchisoniaceans, and foliage-supported lenticular pleurotomariaceans, trilobed plectonotinid bellerophontaceans, and other small gastropods.

A soft-bottom, open lagoon fauna is strongly dominated by deposit-feeding or foliage-dwelling trochiform holopeids, but these give way to small bellerophontaceans nearer shore.

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VARIATION IN THE SILURIAN TABULATE CORAL *PALEOFAVOSITES ASPER*, AND THE STATUS OF *MESOFAVOSITES*

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ABSTRACT. *Paleofavosites asper* (d'Orbigny) is redescribed on the basis of the holotype and additional material from its type area of the Welsh Borderland. The species shows considerable variation, particularly in the form and location of intercorallite pores, from colonies with pores, including a high proportion of solenia, almost exclusively located in corallite angles to those with up to 40% of pores within corallite walls. This species, the type species of *Paleofavosites* Twenhofel, 1914 includes variants with the structural features considered characteristic of *Mesofavosites* Sokolov, 1951. We therefore regard *Mesofavosites* as a junior subjective synonym of *Paleofavosites*.

PALEOFAVOSITES was erected by Twenhofel (1914, p. 24) for favositid corals with intercorallite pores confined in position to corner locations, that is in the angles between corallite walls. Although he was working on material of Ordovician and Silurian age from Anticosti Island, northern Canada, he identified his species with the European *Favosites asper* d'Orbigny, which he therefore chose as the type species for his new genus.

F. aspera [*sic*] d'Orbigny (1850, p. 49) is *F. alveolaris* Lonsdale (*non* Goldfuss) (1839, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b* only). In contrast to Twenhofel's diagnosis for the genus, Jones (1936, p. 15), who redescribed *F. asper*, recorded occasional pores within the walls of corallites of this species in addition to the abundant pores in corner locations. Jones, however, reported the type specimen as lost and based his revision on other material from the Much Wenlock Limestone of Wenlock Edge and Dudley.

Until quite recently, usage of *Paleofavosites* tended to follow the reported character of the type species, with the inclusion in the genus of species with pores in both wall and corner locations as well as those in which pores are restricted to the corallite angles (e.g. Stearn 1956; Hill 1959; Flower 1961). In his important series of papers on Russian tabulate corals, however, Sokolov (1951, p. 59) erected a new genus *Mesofavosites* for favositids with pores in both wall and corner locations and restricted *Paleofavosites* to the terms of Twenhofel's original diagnosis. Since that time, it has become the common practice of Russian workers, and more recently of specialists elsewhere, to follow this usage (Klaamann 1964; Stasińska 1967; Oekentorp and Schouppé 1969; Oekentorp 1971; Stel 1975). Even so, the presence of occasional pores within the walls is accepted in some species of *Paleofavosites* described by these authors, for example, *P. haapsaluensis* Klaamann (Stasińska 1967, p. 69), *P. oelaensis* Klaamann (Stasińska 1967, p. 71), and *P.* sp. a (Stel 1975, pl. 16). Scrutton (1975, p. 29), however, pointed out that if Jones's redescription of *P. asper* is accurate, then *Mesofavosites* should be considered a junior subjective synonym of *Paleofavosites*. If two groups of favositids, one with pores in both wall and corner locations, and the other with pores in corner locations only, are to be distinguished, then it is the group with pores restricted to

[Palaeontology, Vol. 21, Part 2, 1978, pp. 307–319, pls. 28–29]

corner locations that requires the establishment of a new genus. We consider, however, that the range of variation in *P. asper* is such that no generic distinction within this group of corals seems justified.

VARIATION IN PORE POSITION IN *PALEOFAVOSITES ASPER*

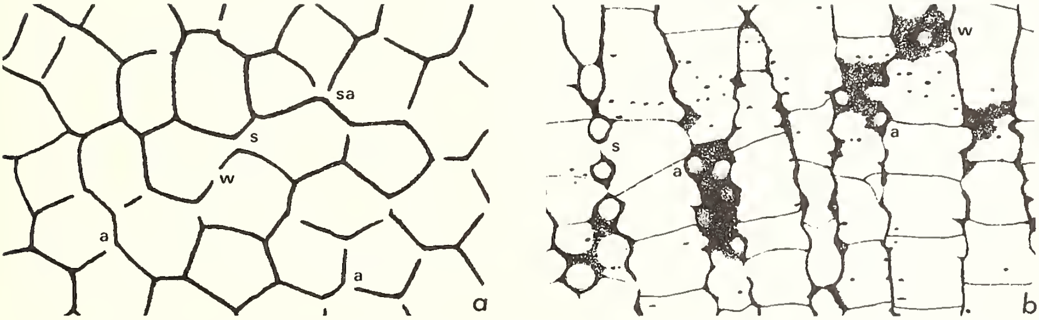
This paper offers a thorough revision of *P. asper* (d'Orbigny) based on a sample of fourteen colonies from the Wenlock and Ludlow Series of the Welsh Borderland and West Midlands. The sample, apart from the holotype and Jones's material, consists of specimens collected by J. H. P. in connection with a revision of British Silurian tabulate corals. The holotype of this species is not missing, as Jones supposed, but is preserved in the Museum of the Institute of Geological Sciences, London (Oekentorp 1971, p. 159). Oekentorp (1976, p. 168) has recently redescribed the holotype only of *P. asper* in the course of a valuable contribution on the definition of the previously confused species *P. asper*, *P. alveolaris* (Goldfuss), and *P. alveolaris sensu* Lonsdale (*non* Goldfuss) (1839, pl. 15 *bis*, fig. 2, 2*a* only) which he assigned to *P. rugosus* Sokolov. He discussed at length the problem of the significance of pore morphology and location but reported no definite pores within the walls of the holotype of *P. asper* and he left the status of *Mesofavosites* open. We are able to demonstrate, however, the presence of occasional pores within the walls of the holotype (Pl. 28, fig. 2). In addition, there is a range among other material of the same species from the Much Wenlock Limestone and Aymestry Limestone of the Welsh Borderland and West Midlands from colonies in which pores in wall locations are extremely rare, to those in which they constitute 40% of pores seen in cross-section (Table 1).

Three varieties of pores are present in the species as a whole, although two types dominate in most colonies. Pores in corner locations are either *solenia*, short tubular pores linking opposite corallites where four corallites meet at a common junction, or *angle pores* linking adjacent corallites (text-fig. 1). In vertical series solenia alternate in orientation through 90°, linking first one pair and then the other pair of opposite corallites to produce a very characteristic pattern in longitudinal section (text-fig. 1*b*; Stel and Oekentorp 1976, fig. 3). Solenia are present in all specimens assigned here to *P. asper*, although they are very rare in BMNH R49779 and R49780. Angle pores are defined as developed in the lateral margin of a corallite wall such that in cross-section they appear bounded by the wall in which they occur on one side only. Such pores are present and common throughout. The third variety of pore is the *wall pore*, contained entirely within one corallite wall (text-fig. 1). These are very rare in nearly half the colonies of *P. asper* described here (Table 1). All three varieties of pores are present in the holotype (Pl. 28, fig. 2). The three pore forms described could all be considered as varieties of mural pores, but there is descriptive value in distinguishing solenia from mural pores in wall and angle locations. The term mural pores is used in this paper in this sense, that is for angle pores and wall pores together.

Within the species, the pores appear to form a continuous morphological series. Solenia can only form at the junction of four corallites. Occasionally 'sub-solenioid' arrangements of angle pores, when a solenium is replaced by one or two angle pores at four corallite junctions, are seen in cross-section, linking these two pore types (text-fig. 1*a*; Pl. 28, fig. 5; Pl. 29, fig. 2). Angle pores at three- and four-wall junctions are as

TABLE 1. Data for the individual colonies and total sample of *Paleofavosites asper*. Although in three colonies, no wall pores were observed within the 2 sq. cm. area from which pore percentages were calculated (indicated by asterisks), in each case at least one wall pore was observed in cross-section outside this area. N = number of corallites; O.R. = over-all range; x̄ = mean; s = standard deviation.

Specimen No.	Corallite Diameter (mm)				Tabulae per 5mm		Angle Pores mean diam (mm)	Pore Percentages in 2 sq cm cross section		
	N	O.R.	x̄	s	unthickened zone	thickened zone		Solenia :	Angle Pores :	Wall Pores
BMNH R49785	40	0·89 - 1·16	1·02	0·060	5	11	0·16	26	74	0*
BMNH R49787	40	1·02 - 1·32	1·13	0·086	6	10	0·19	22	78	0*
BMNH R49788	40	0·92 - 1·35	1·12	0·081	6	13	0·19	19	81	0*
BMNH R26302 (figd Jones 1936)	40	0·70 - 1·15	0·94	0·087	7	12	0·16	39	60	1
BMNH R49784	40	0·85 - 1·28	1·12	0·129	6	9	0·19	31	68	1
BMNH R49781	40	0·85 - 1·15	1·03	0·066	10	18	0·18	8	91	1
BMNH R49782	40	0·92 - 1·19	1·04	0·069	7	12	0·14	8	89	3
BMNH R49783	40	0·99 - 1·20	1·09	0·050	7	15	0·17	17	79	4
BMNH R49780	40	0·92 - 1·28	1·03	0·087	10	15	0·16	2	91	7
BMNH R49778	40	0·80 - 0·95	0·87	0·034	6	12	0·14	6	85	9
GSM GSb 3728 (holotype)	40	0·90 - 1·29	1·08	0·087	3	6	0·20	12	77	11
BMNH R49786	40	0·86 - 1·12	1·01	0·064	12	15	0·15	7	81	12
BMNH R49779	40	0·87 - 1·21	0·98	0·059	4	12	0·17	2	65	33
BMNH R26559 (descr. Jones 1936)	40	0·92 - 1·35	1·10	0·101	9	23	0·15	5	55	40
TOTAL SAMPLE	560	0·70 - 1·35	1·04	0·079	range 3-12	range 6-23	range 0·14-0·20			



TEXT-FIG. 1. Pore types in *Paleofavosites* in (*a*) cross-section, and (*b*) longitudinal section. s = solenium; sa = 'sub-solenioid' angle pore; a = angle pore; w = wall pore. × 10.

closely packed in vertical series as solenia and are associated with walls with strongly corrugated lateral margins. There is a complete range from angle pores of this description to those in which their vertical spacing is increased, and the wall margins are progressively less corrugated. This can be seen both between and within colonies, whilst in BMNH R26559 wall margins are almost always straight (Pl. 29, fig. 6). Wall pores also show a complete range from locations close to wall junctions to mid-wall situations.

THE STATUS OF *MESOFAVOSITES*

The principal factor in the diagnosis of *Mesofavosites* has been the presence of pores in both angle and wall locations. In addition, the type species, *M. dualis* Sokolov (1951, p. 61, pl. 22, figs. 1–5; pl. 23, figs. 1–2), appears to lack solenia and strongly crenulate wall margins in longitudinal section, although little information on variation in this species is currently available. All of these features, except the total lack of solenia, occur in variants of *P. asper* and none of them can be used as a secure foundation for a generic distinction between *Mesofavosites* and *Paleofavosites*. The absence of solenia may be a function of corallite size as suggested by Stel and Oekentorp (1976, p. 169), with four corallite junctions rare in favositids with larger corallites. There are a number of species with larger corallites assigned to *Paleofavosites* that lack solenia. Furthermore, although Stel and Oekentorp (1976, p. 165) consider the lack of laterally crenulate walls associated with angle pores as distinctive of *Mesofavosites*, this condition is seen in the sample of *P. asper* described here (BMNH R26559). Finally, the corallite walls of *M. dualis* are corrugated in cross-section. Sokolov himself, however, assigned species with straight corallite walls to *Mesofavosites* (*M. multiporus* Sokolov, 1951, p. 69, pl. 29, figs. 3–4) and species with crenulate walls to *Paleofavosites* (*P. legibilis* Sokolov, 1951, p. 13, pl. 2, figs. 7–9; pl. 3, figs. 1–2) and this feature is clearly not of generic significance.

We conclude therefore that *Paleofavosites* should be interpreted broadly to include species with both wall pores and angle pores, as well as those with angle pores only, with or without the development of solenia. In view of the considerable infraspecific variability in pore form and location in the type species, we believe that there is no justification for erecting any generic subdivision within this group of favositids. We consider *Mesofavosites* to be a junior subjective synonym of *Paleofavosites*. In addition, Stel and Oekentorp (1976) have argued that *Multisolenia* Fritz, 1937, *Mesosolenia* Mironova, 1960, *Priscosolenia* Sokolov, 1962 and *Sparsisolenia* Stasińska, 1967, genera based on variations in the development of solenia, are also junior subjective synonyms

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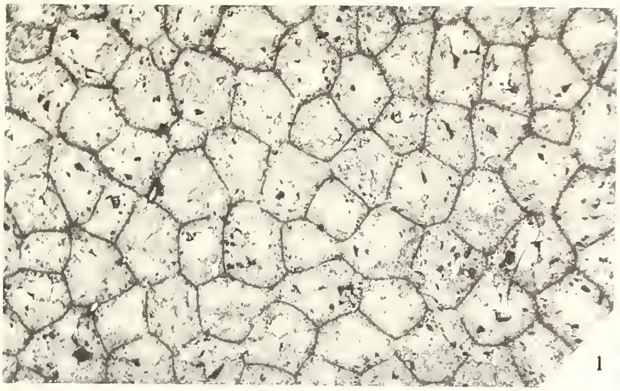
EXPLANATION OF PLATE 28

Figs. 1–7. *Paleofavosites asper* (d'Orbigny). 1–2, GSM PF 4787; 3, GSM PF 4788 (holotype). Silurian, Aymestry Limestone, Leinthall Earls, near Aymestrey, Hereford and Worcester. 1, cross-section, × 8; 2, cross-section showing a solenium, wall pore, and angle pore closely associated (slightly left of centre), × 16; 3, longitudinal section showing solenia and angle pores, × 8; 4–5, BMNH R49781a; 6–7, BMNH R49781b. Silurian, Much Wenlock Limestone, Shadwell Rock Quarry, Much Wenlock, Salop. 4, cross-section of colony with well-developed septal spines, × 8; 5, cross-section showing a solenium (left centre) and a 'sub-solenioid' angle pore (right centre), × 16; 6, longitudinal section, × 8; 7, detail of part of fig. 6 showing a wall pore and angle pores, × 16.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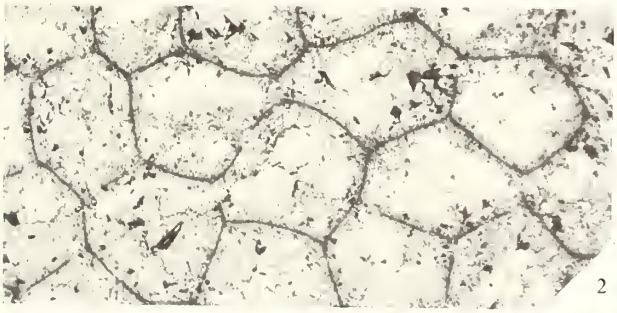
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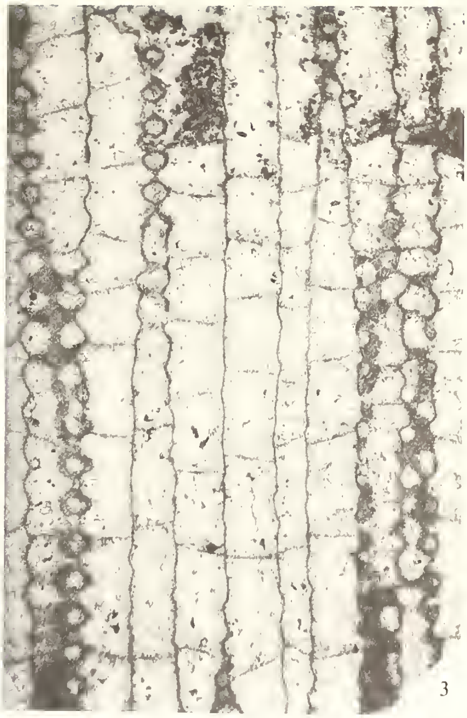
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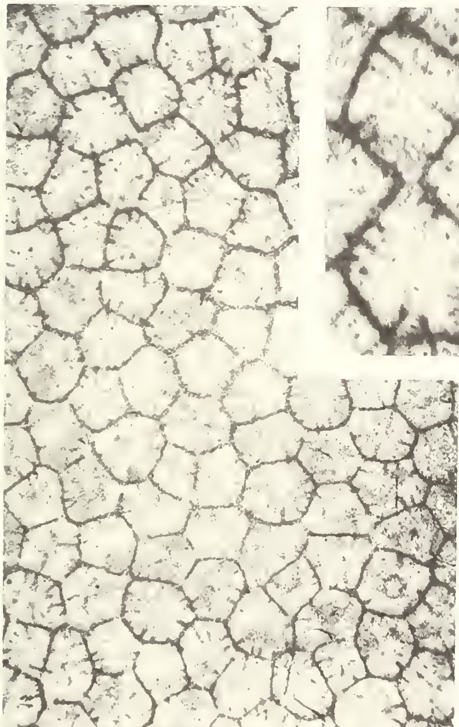
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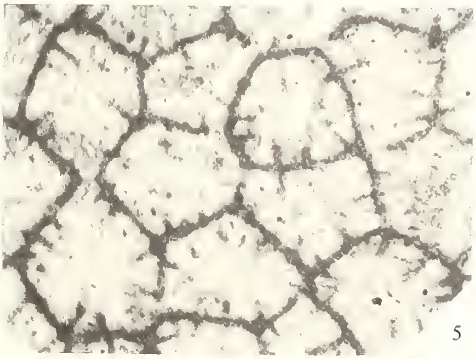
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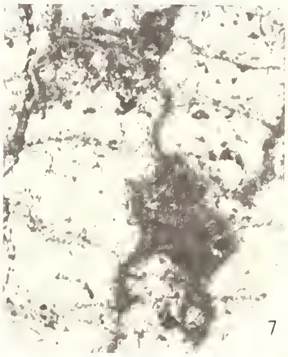
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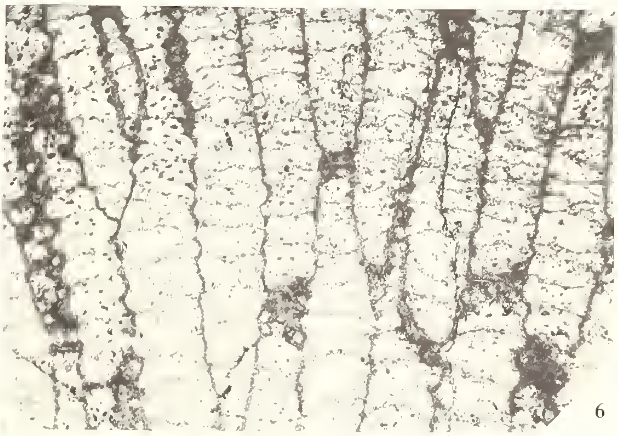
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POWELL and SCRUTTON, *Paleofavosites asper* of *Paleofavosites*. Although we have not specifically studied examples of these genera, we support these synonymies on the basis of the published information and our observations on *Paleofavosites asper*. Stel and Oekentorp (1976, p. 173), however, go further and suggest that *Multisolenia* is a synonym of *Desmidopora* (Nicholson 1886) and that *Desmidopora* should be maintained as a subgeneric division within *Paleofavosites*. From published information, and in the absence of a full redescription of the type species *D. alveolaris* Nicholson we are not convinced that *Desmidopora* is a paleofavositid: we understand that redescription of *D. alveolaris* is intended for subsequent publication by Stel and Oekentorp (Stel, pers. comm. to J. H. P.). In the meantime, we would point out that if *Desmidopora* and *Paleofavosites* are accepted as congeneric subgenera, then *Desmidopora* has priority and they should be designated *Desmidopora* (*Desmidopora*) and *Desmidopora* (*Paleofavosites*), not as given by Stel and Oekentorp (1976, p. 173) (see I.C.Z.N., Art. 23e).

Our study of *P. asper* illustrates the highly variable nature of favositid species as demonstrated by most work on large samples of these corals (e.g. Philip 1960). Other favositid species from the Welsh Borderland at present under study by J. H. P. also show this tendency to high variability, with adult corallite diameter the least-affected character and apparently the most useful primary species discriminator. Over the years a very large number of favositid species have been erected, often on only a single specimen or a very small sample. It is highly likely that many of these are synonyms and there is a great need for more variation studies of substantial populations of favositids to bring species discrimination in this group to a more realistic level and to stabilize generic concepts.

SYSTEMATIC DESCRIPTIONS

Order TABULATA Edwards and Haime, 1850
Suborder FAVOSITINA Sokolov, 1962
Family FAVOSITIDAE Dana, 1846
Genus PALEOFAVOSITES Twenhofel, 1914

1914 *Paleofavosites* Twenhofel, p. 24.
e.p. 1936 *Favosites*; Jones, p. 2.
1937 *Multisolenia* Fritz, p. 231.
1940 *Palaeofavosites*; Lang, Smith and Thomas, p. 94.
1951 *Palaeofavosites*; Sokolov, p. 12.
1951 *Multisolenia*; Sokolov, p. 50.
1951 *Mesofavosites* Sokolov, p. 59.
1955 *Palaeofavosites*; Sokolov, p. 153.
1955 *Mesofavosites*; Sokolov, p. 153.
1955 *Multisolenia*; Sokolov, p. 153.
1956 *Paleofavosites*; Stearn, p. 59.
1959 *Paleofavosites*; Hill, p. 11.
1960 *Mesosolenia* Mironova, p. 95.
1961 *Paleofavosites*; Flower, p. 71.
1962 *Priscosolenia* Sokolov, p. 58.
1964 *Palaeofavosites*; Klaamann, p. 5.
1964 *Priscosolenia*; Klaamann, p. 40.
1964 *Multisolenia*; Klaamann, p. 42.
1964 *Mesofavosites*; Klaamann, p. 45.

1967 *Palaeofavosites*; Stasińska, p. 66.
1967 *Priscosolenia*; Stasińska, p. 73.
1967 *Sparsisolenia* Stasińska, p. 74.
1967 *Multisolenia*; Stasińska, p. 75.
1967 *Mesofavosites*; Stasińska, p. 76.
1971 *Palaeofavosites*; Oekentorp, p. 158.
1975 *Paleofavosites*; Scrutton, p. 29.
1975 *Palaeofavosites*; Stel, p. 41.
1975 *Priscosolenia*; Stel, p. 55.
1975 *Multisolenia*; Stel, p. 61.
1975 *Mesofavosites*; Stel, p. 65.
1976 *Paleofavosites*; Oekentorp, p. 165 (see for extensive synonymy excluding *Mesofavosites*).

Type species (by original designation). *Favosites aspera* [*sic*] d'Orbigny 1850, p. 49 = *F. alveolaris* Lonsdale (*non* Goldfuss) 1839, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b*, *non* fig. 2, 2*a*.

Diagnosis. Massive, ramose, foliaceous, or encrusting cerioid tabulate corals. Corallites generally contiguous, polygonal, of similar diameter throughout much of their length. Angle pores characteristic but solenia and/or wall pores may also be present in varying proportions. Septal spines present in some species, variably developed, usually in vertical rows. Squamulae also variably developed in some species, with or without associated septal spines. Squamulae and septal spines in the same species usually intergrade. Tabulae generally flat, complete. Increase lateral.

Remarks. As Caramanica (1975) has recently pointed out, the correct, original spelling of the generic name is *Paleofavosites* and not *Palaeofavosites* as used by many authors including Oekentorp (1971) in his submission to the I.C.Z.N. The ruling in favour of the validation of the generic name by the Commission meant that the incorrect spelling was initially placed on the Official List of Generic Names (Opinion 1059). This has since been corrected in *Bull. zool. Nomencl.* **33,** 3/4 (1977), 264.

Paleofavosites asper (d'Orbigny, 1850)

Plate 28, figs. 1–7; Plate 29, figs. 1–6; text-fig. 2; Table 1

non 1829 *Calamopora alveolaris* Goldfuss, p. 77, pl. 26, figs. 1*a–c*.
e.p. 1839 *Favosites alveolaris* (de Blainville) Lonsdale, p. 681, pl. 15 *bis*, fig. 1, 1*a*, 1*b*, *non* fig. 2, 2*a*.
1850 *Favosites aspera* d'Orbigny, p. 49.
non 1851 *Favosites aspera* d'Orbigny; Edwards and Haime, p. 234.
e.p. 1855 *Favosites aspera* d'Orbigny; Edwards and Haime, p. 257, pl. 60, fig. 3, 3*a*.
1914 *Paleofavosites aspera* (d'Orbigny) Twenhofel, p. 24.
1936 *Favosites asper* d'Orbigny; Jones, p. 15, pl. 2, figs. 1–3.
1971 *Palaeofavosites asper* (d'Orbigny); Oekentorp, p. 158.
1976 *Paleofavosites asper* (d'Orbigny); Oekentorp, p. 168, pl. 19, figs. 1–9; pl. 20, figs. 1–3; pl. 21, figs. 7–8, *cum syn.*

Holotype. GSM GSb 3726–3728 (parts of one specimen; slides GSM PF 4548–4551, peels GSM PF 4787–4788). Silurian, Ludlow Series, Aymestry Limestone; Leinthall Earls, 3·2 km NNE. of Aymestry, Hereford and Worcester.

The horizon and locality were given as 'Wenlock Limestone, Leinthall Earls' by Lonsdale (1839, p. 681). The large quarry at Leinthall Earls (SO 44306810), however, is in the Aymestry Limestone (Bringewood Beds) of the Ludlow Series. *P. asper* has been found by us in this quarry (BMNH R49778–49779) and the preservation of the material closely matches that of the holotype. The nearest outcrop of the Much Wenlock Limestone to yield *P. asper* in the present investigation was at Pitch Coppice (SO 47297300), 6 km NE. of Leinthall Earls where the preservation is less similar to that of the holotype. We conclude, therefore, that the horizon of the holotype was wrongly stated by Lonsdale.

Additional material. Silurian, Ludlow Series, Aymestry Limestone: BMNH R49778–49779, large working quarry, Leinthall Earls, Hereford and Worcester (SO 44306810).

Silurian, Wenlock Series, Much Wenlock Limestone: BMNH R26559 and R49780, Farley Quarry, 1·7 km N. of Much Wenlock, Salop (SJ 62900152); BMNH R49781, Shadwell Rock Quarry, 1 km N. of Much Wenlock, Salop (SJ 62620090); BMNH R49782–49783, outcrop in field 120 m W. of Lower Dinchope–Westhope Road, 685 m from Lower Dinchope, near Craven Arms, Salop (SO 45228495); BMNH R49784, disused quarry in Pitch Coppice, near Ludlow, Salop (SO 47297300); BMNH R26302, Dudley, West Midlands.

Silurian, Wenlock Series, Edgton Limestone: BMNH R49785–49788, track to Thrushes Mead, Ridgeway Wood, near Edgton, Salop (SO 39928645).

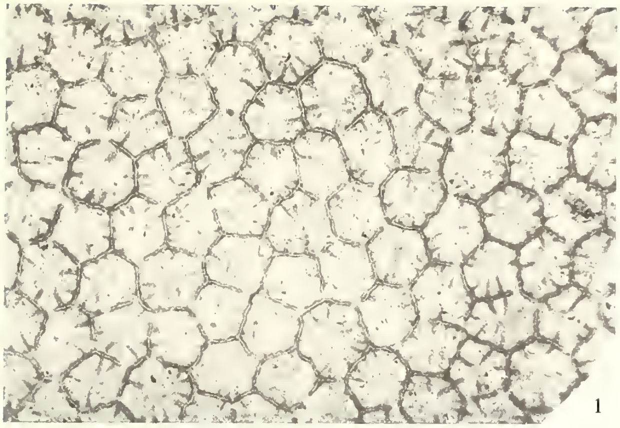
Diagnosis. Paleofavosites of lamellar to broadly-domed growth form with mean adult corallite diameter in the range 0·87–1·13 mm. Colonies may have regularly developed growth zones of thickened skeletal elements. Corallite wall thickness variable within and between colonies, from 0·09 mm in unthickened zones to 0·15 mm in thickened zones. Septal spines and squamulae very variably developed and intergrading; both more common in thickened zones and rare to absent elsewhere. Angle pores common, solenia usually well developed but occasionally rare, wall pores very rare to moderately common. Pores 0·14–0·20 mm mean diameter. Tabulae complete, horizontal; spacing variable from 3 in 5 mm in unthickened zones to 23 in 5 mm in thickened zones.

Description. The holotype, now in four parts, was an approximately broadly-domed colony 120 mm diameter by 70 mm high. Other specimens range from lamellar to broadly-domed in growth form and reach a maximum size of 230 mm diameter by 80 mm high.

The corallites are polygonal in cross-section, 3–4 sided when immature, 4–7 sided in adult stages. Mean corallite diameter of the sample is 1·04 mm and ranges in colonies from 0·87 to 1·13 mm. Corallite walls are thin in the holotype, 0·09–0·12 mm thick, consisting of an axial plate, 0·02–0·03 mm thick, coated on either side by fibronormal tissue. Regular growth zones of skeletal thickening are present but these are more prominent in most of the other material. They have a vertical frequency of between 4 and 12 mm and walls may reach 0·20 mm thick in thickened zones. Septal spines and flattened, squamulate spines are very variably developed and one form grades into the other. Both are more prominent or sometimes only developed in the thickened zones but even here are usually present only around part of the periphery of any one corallite. Up to twelve spines/squamulae per corallite have been counted in cross-section. They

EXPLANATION OF PLATE 29

Figs. 1–6. *Paleofavosites asper* (d'Orbigny). 1–2, BMNH R49780a; 3, BMNH R49780b; 4–5, BMNH R26559c; 6, BMNH R26559d. Silurian, Much Wenlock Limestone, Farley Quarry, Much Wenlock, Salop. 1, cross-section cut through zone of thickening of colony with well-developed septal spines, × 8; 2, cross-section showing solenium (centre), wall pores (centre and right centre), 'sub-solenioid' angle pore (right top), and several other angle pores, × 16; 3, longitudinal section, × 8; 4, cross-section of colony with more weakly developed septal spines, × 8; 5, cross-section showing a solenium (right of centre), angle pores and several wall pores, × 16; 6, longitudinal section showing relatively straight walls and wall pores, × 8.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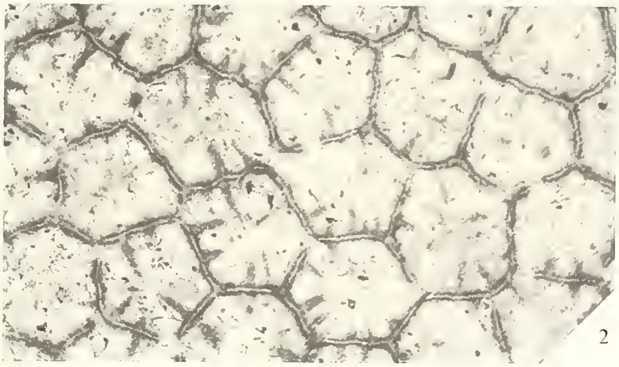
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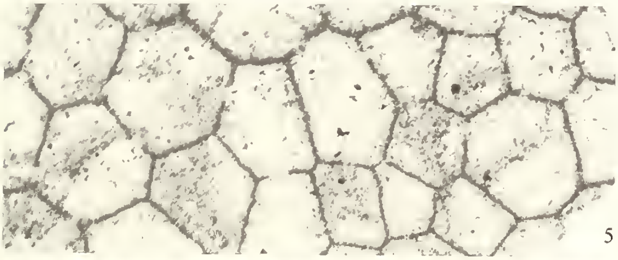
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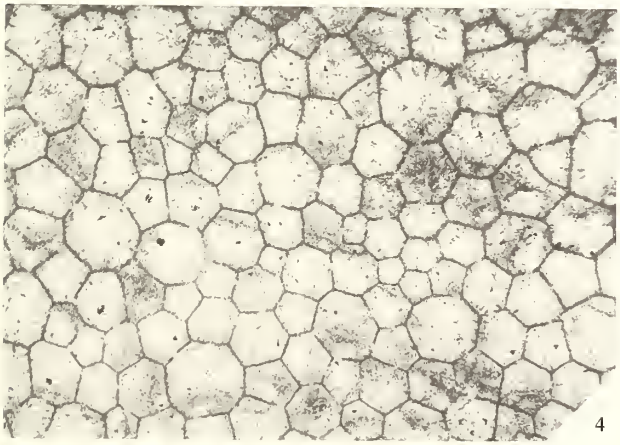
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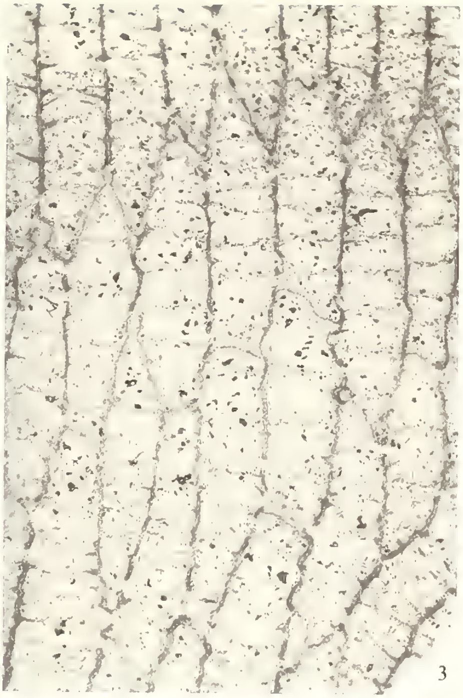
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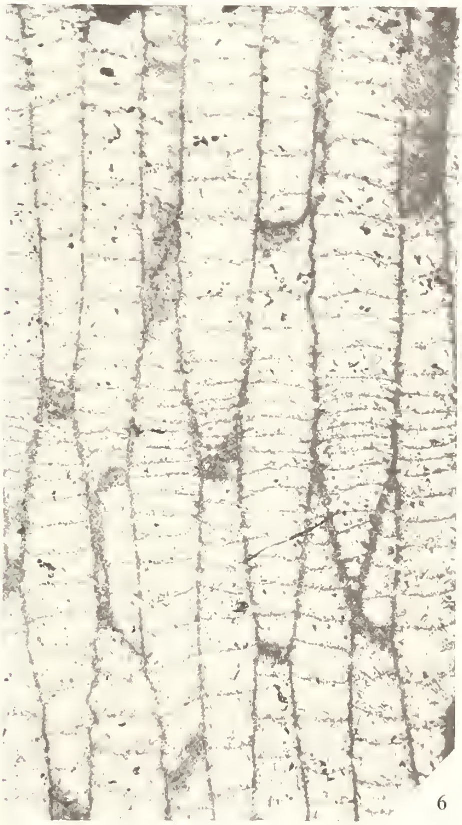
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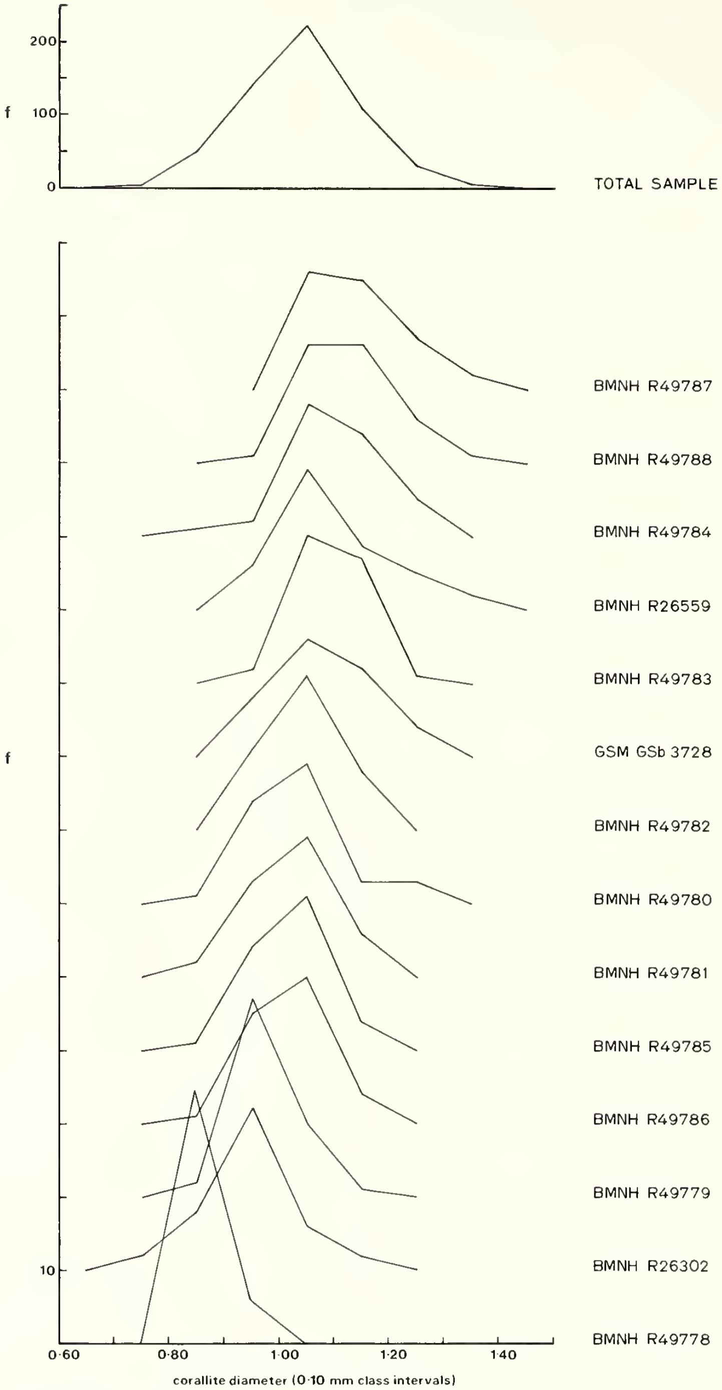
POWELL and SCRUTTON, *Paleofavosites asper*



TEXT-FIG. 2. Corallite diameter—frequency polygons for the individual colonies and total sample of *Paleofavosites asper*. In the lower series of polygons, each division on the abscissa is equivalent to ten corallites.

may vary from short, thin spines to stout, blunt projections up to 0·5 mm long. Intercorallites connections are in the form of solenia and mural pores (angle pores and wall pores). In a 2 sq. cm. cross-section, there are 55–91% angle pores, 2–39% solenia, and up to 40% wall pores in the material studied (Table 1). Solenia tend to be more common when wall pores are rare. Mural pores and solenia may be sealed by a pore plate.

In longitudinal section, tabulae are complete, horizontal to slightly concave upwards. Zones of closely spaced tabulae coincide with more numerous, thickened septal spines and thickened corallite walls. Tabulae spacing varies from 6–23 in 5 mm in thickened zones to 3–10 in 5 mm in unthickened zones. Mural pores are circular, 0·14–0·20 mm mean diameter in different colonies with a vertical spacing of 0·35–0·40 mm. Wall pores appear only rarely in the plane of section. Angle pores are usually associated with longitudinally crenulated wall margins, although in some specimens the crenulation may be slight or even absent. Solenia appear as a vertical series of regularly spaced but unconnected rings of skeletal tissue. Septal spines/squamulae are directed horizontally or slightly upwards into the lumen. A circular cross-section is more common than a flattened one, and some spines may change from the former to the latter along their length.

Discussion. Data for the sample described here are listed in Table 1 and illustrated in text-fig. 2. We have used the formula given by Sutton (1966) for the 'diameter' of a polygonal corallite, that is half the sum of the maximum corner-to-corner measurement and the minimum wall-to-wall measurement for each corallite.

P. asper is a very variable species. We regard the development of regular thickened growth zones in these colonies as an environmental feature reflecting an annual climatic cycle. The variation in the development of the septal processes and the spacing of the tabulae is associated with this periodicity, and these morphological elements therefore have limited taxonomic value at the species level in this group of corals. Septal processes are particularly variable in form in *P. asper* to the extent that spines and squamulae show complete intergradation. This is in agreement with Philip's (1960) conclusions that squamulae are modified septal spines subject to environmentally induced variation and of little taxonomic significance. Adult corallite diameter is much less variable and appears to be a more reliable first criterion for species discrimination. Similar conclusions were reached by Sutton (1966).

Schouppé and Oekentorp (1974) also suggested that pore diameter in favositids remains constant within the species and may be of taxonomic value. We find, however, a considerable variation in mean pore diameter from colony to colony of this species (Table 1). Neither is there a strong correlation of mean pore diameter with mean corallite diameter ($r = 0{\cdot}58$).

The feature of this species which we most wish to stress is the considerable variation in pore distribution. Although the proportions of different pore types show little variation from place to place within a colony, there is considerable variation between colonies (Table 1). Other species of *Paleofavosites* from the Welsh Borderland show similar variation in pore location.

P. asper is distinguished from *P. rugosus* Sokolov (= *F. alveolaris* Lonsdale (*non* Goldfuss) 1839, pl. 15 *bis*, fig. 2, 2*a*), which is also present in the Much Wenlock

Limestone of the Welsh Borderland, by its smaller mean corallite diameter (Oekentorp 1976, p. 172). *P. rugosus* in the Welsh Borderland sample has adult corallite diameters in the range 2·10–2·60 mm.

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ORIGINAL STRUCTURE AND COMPOSITION OF PERMIAN RUGOSE AND TRIASSIC SCLERACTINIAN CORALS

by JAMES E. SORAUF

ABSTRACT. Rugose corals from the Permian of Timor (Indonesia) and scleractinian corals from the Triassic of northern Italy are both exceptionally well preserved. The scleractinians, as shown previously by Montanaro Gallitelli, are preserved as the original aragonite. They have skeletal structures virtually identical to those in living corals, with some minor diagenetic alteration but without change in mineralogy. Microprobe scan lines show strontium as the common minor element in the Triassic skeletal aragonite. The rugosans studied were selected as the best-preserved available Permian corals, from Basleo, Timor. Small crystal sizes within calcitic skeletal micro-structure and perfect development of trabecular septal structure, as shown by scanning electron microscopy in polished and etched sections and also in broken sections, suggest little diagenetic alteration in some specimens. Where diagenetic structures are recognizable (as in walls of *Polycoelia*) they are obviously discordant with primary biogenic structures. Skeletal carbonate with little or no observable diagenetic alteration at the electron microscopic level is lacking in both strontium and magnesium as minor elements, suggesting that low magnesian calcite, rather than aragonite was the primary skeletal mineral composition in these Permian corals.

RESULTS of a comparative study of the structure and composition of Permian and Triassic corals are presented here. The question to be answered is whether there was originally a great difference between Permian rugose corals and early scleractinian corals. Palaeontologists, carbonate petrologists, and geochemists are all concerned with possible differences in coral structure and mineralogy and, by inference, with possible differences in metabolic processes or protein chemistry or sea-water chemistry. A number of authors have commented on this question, but the opinion has almost always been based merely on the apparent quality of preservation of fossil corals; the only exception is the work of Lowenstam, who reported on the composition of several rugose corals (1963, p. 187).

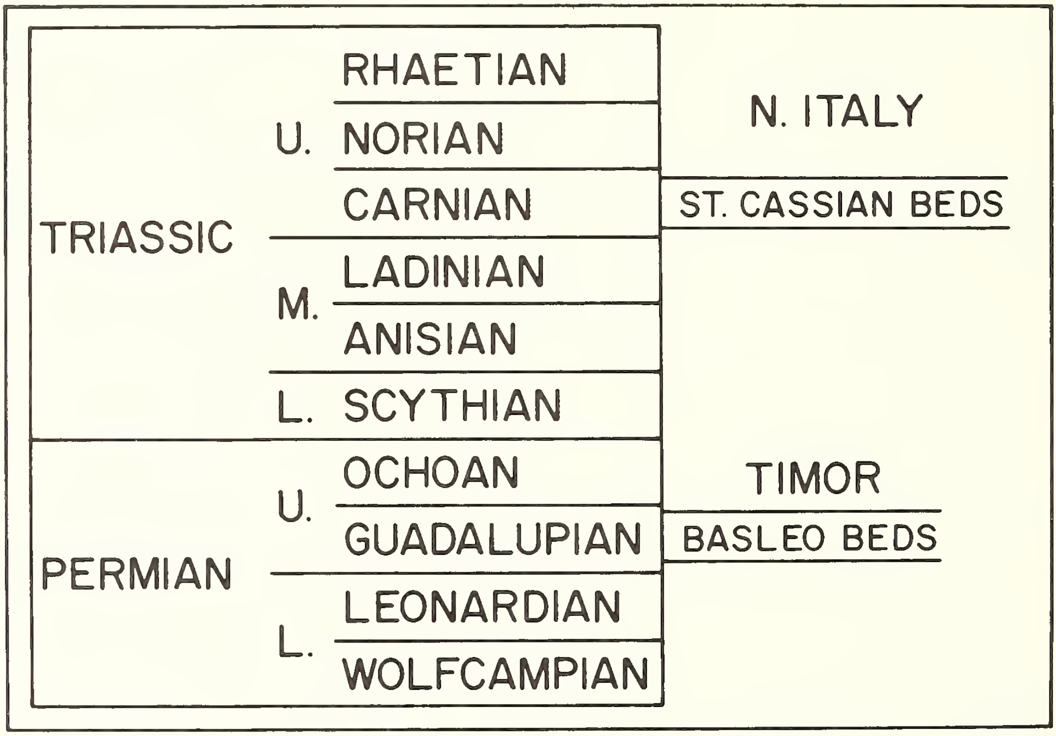
In order to make meaningful statements regarding mineralogy, composition, and possible recrystallization, one must first, know a reasonable amount regarding diagenetic processes that may have been operative during the history of burial and fossilization, and second, both understand rather precisely the formation and patterns of biogenic structures in the coral skeleton in living and fossil scleractinians, and also have empirical data regarding the microstructure of the rugosan skeleton. This includes the means of assessing structures as to their biogenic origin or later development due to diagenetic alteration of carbonates. Such information is here used in the comparison of very well-preserved Upper Permian (Guadalupian) corals from the island of Timor with exceptionally well-preserved Late Triassic (Carnian) corals of northern Italy (text-fig. 1). The primary sources of this data are the scanning electron microscope and the electron microprobe.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 321–339, pls. 30–33.]

MATERIAL

The Permian fossils from the island of Timor are justly famous for their excellent preservation and are also of great interest due to the variety and make-up of this late Palaeozoic fauna. As one can note in the published literature, especially on the photographic plates of Schindewolf (1942), details of coral skeletal structures are excellently preserved. A few exceptionally well-preserved Permian specimens were thus chosen during a visit to the Geologisches-Paläontologisches Institut at the Friedrich Wilhelm University at Münster, which houses a large collection of Permian corals from Timor. These were collected by J. Wanner during expeditions in 1909 and 1911 and have been recently studied by Schouppé and Stacul (1955, 1959) and by Nierman (1975). The specimens that are reported on here are all from the Basleo 23 collecting locality.

Aragonitic Triassic scleractinian corals have been reported from northern Italy by Montanaro Gallitelli (1973, 1974) and studied taxonomically and for their microstructure. Her fauna, collected from near Cortina d'Ampezzo has also been studied for strontium content in some detail by Montanaro Gallitelli, Morandi, and Pirani (1973). The specimens included in the present study were collected by the writer at the 'Sett Sass' locality (Ogilvie Gordon 1929, p. 399). The specimens were determined by X-ray



TEXT-FIG. 1. Permian and Triassic stages, with chronostratigraphic position of the St. Cassian strata from the Dolomiti and the Basleo beds of Timor.

diffraction to be aragonite, and have provided data on the location of minor elements and microstructure of exceptionally well-preserved scleractinian corals to compare with the Permian corals of Timor.

Illustrated specimens are in one of two repositories. The Triassic specimens from this paper are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Permian specimens are in the Geologisches-Paläontologisches Institut, Münster (G-PMM).

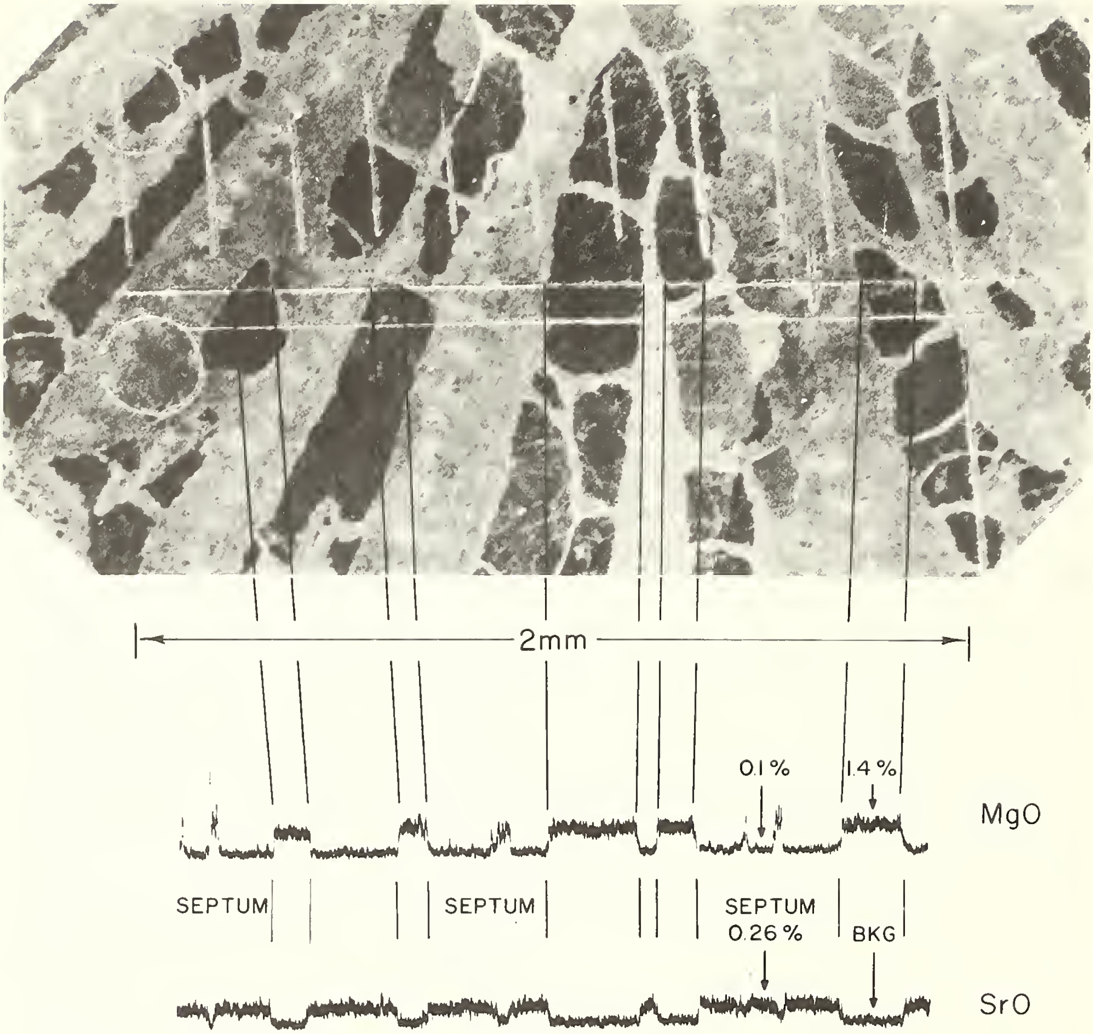
METHODS OF INVESTIGATION

This study attempts to locate precisely the distribution of minor elements in the skeletal carbonate and in interskeletal void-filling carbonate. Thus, specimens selected for intensive study were first thin-sectioned and one sawed surface was then polished for study with the electron microprobe. After polishing, lines were scribed for the traverse path and for a scale, utilizing a centred diamond stylus mounted in place of an objective lens on a metalographic microscope. After the microprobe traverse had been run, analysing for strontium and magnesium, the specimen was lightly etched for study in the scanning electron microscope. This light etch not only retained the scribe markings for scale and path, but also etched into visibility the microprobe traverse line (text-fig. 2), where carbonate has been partially destroyed by the electron beam. In addition, skeletal and interskeletal carbonate has been variably etched, so that biogenic elements can be easily differentiated from the calcitic spar filling interseptal spaces. This system allowed for exact correlation of data from microprobe scan lines and individual elements of each coral. After correlation, the specimens were polished lightly once again to remove traces of scribed lines, and then etched with 0·1 normal formic acid for study of structures within the scanning electron microscope.

It should also be noted that some of the Permian specimens from Basleo are so well preserved that they could be successfully studied in broken sections by means of the scanning electron microscope. Small crystal sizes and an apparent lack of recrystallization allow detailed study of skeletal structure by this method, which has not been of value in the study of Palaeozoic corals.

TRIASSIC SCLERACTINIAN CORALS

Triassic corals were collected by me from the St. Cassian strata (Carnian Age) during visits to the Dolomiti of northern Italy (1961, 1975). The collections were made from brownish shales where they overlay the famous dolomitized Richthofen Reef (Ogilvie Gordon 1929, p. 399). This is the locality referred to as 'Forcella di Sett Sass' by Volz (1895, p. 100). Of a number of corals collected by me from this locality, one colony of *Thecosmilia*, apparently that named *T. badiotica* by Volz (1895, p. 26) was chosen for detailed microprobe analysis and scanning electron microscopy. Further microscopy was carried out on biogenic structures in a colony of *Isastraea* cf. *I. gumbeli* Laube 1865. Both specimens have skeletal elements composed of aragonite, as shown by X-ray diffraction.



TEXT-FIG. 2. *Thecosmilia badiotica* (USNM 245274). Composite micrographs to show septa, dissepiments, and spar filling former void spaces. Scribed lines show the start (with a circle), path, and finish of the scale and traverse line, marked by a long bar. The microprobe traverse line has been etched into prominence, lies between the scribed lines, and can be identified by the black lines drawn to it from below. Below are noted traverse elemental scan lines for magnesium and strontium, as well as semi-quantitative analyses at the points shown. Note that each septum is marked by a line of trabecular centres which also make themselves evident in the microprobe analysis by their anomalous content of magnesium and strontium.

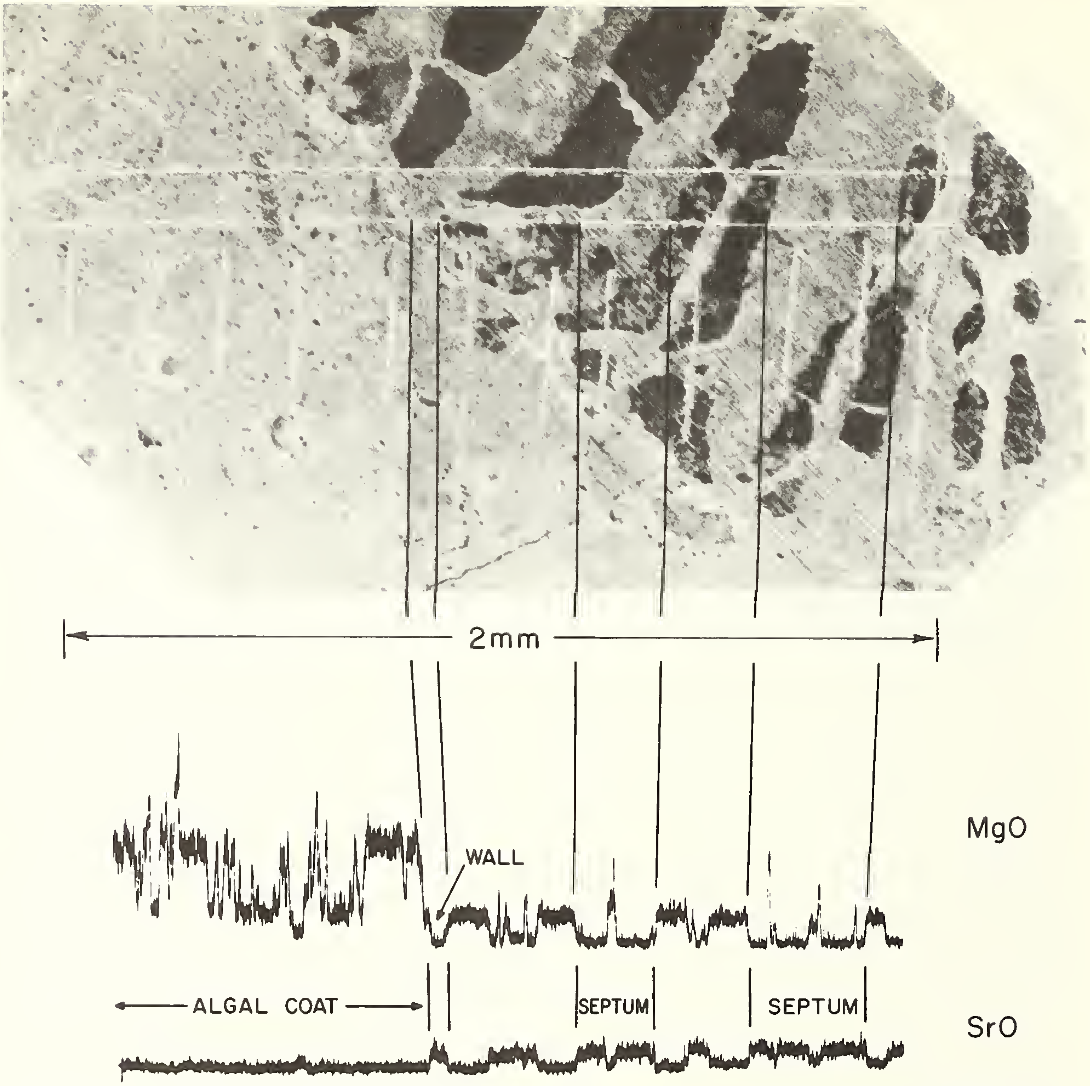
Thecosmilia badiotica Volz

This specimen of *Thecosmilia* is part of a large colony. Unfortunately, the thin-section is just within a budding sequence (Pl. 30, fig. 1) and is thus elongate and difficult to recognize as that form referred to as *T. badiotica* by Volz (1895, p. 26). Microprobe traverses were run in two widely separated areas and the area, the trace, and the analysis for each is shown (text-figs. 2 and 3). As can be seen in the first of these figures, the etched surface shown in the scanning electron micrograph (SEM) clearly differentiates between skeletal carbonate and the sparry infilling (calcitic) between skeletal elements. The skeletal aragonite and sparry calcite are mirror images with respect to the occurrence of magnesium and strontium, with the skeletal aragonite being relatively high in SrO (approx. 0·25% by weight) and reading at background count to show the absence of magnesium. The calcitic spar is as high as 1·4% MgO by weight by reading at or close to background for strontium content. It is also noticeable here that spikes occur in the minor element contents in the centres of the septa. This suggests strongly that these trabecular centres of the septa are altered. As was noted for Pleistocene corals from Barbados, alteration of septal aragonite commonly commences at the centres of the finely crystalline septal trabeculae (James 1974, p. 790). Text-fig. 3 is another composite SEM with correlative microprobe traces, with the scan line (probe) beginning in a calcitic algal coating of the corallite and progressing into the corallite interior. Here it can be seen once again that the skeletal aragonite contains strontium, that the sparry calcitic infilling has some magnesium, but much less than that of the calcitic algal coating, and what are apparently recrystallized trabecular centres show as spikes on the microprobe traverse for MgO as it crosses the septum.

The same surface, repolished and re-etched prior to study in the scanning electron microscope, provides evidence on the structure of skeletal features in this Triassic coral. The septa are finely trabecular (in thin-section view showing the central 'dark line') with good preservation of trabecular centres (Pl. 30, fig. 2), and within trabecular centres there are small radiating crystals as well as evidence of some small amount of recrystallization (Pl. 30, fig. 3). Dissepiments likewise show a feature characteristic of modern corals with crystal growth from the bordering septa to a centre line, with a junction groove (Sorauf 1970, p. 7) shown on the undersurface of the dissepiment (Pl. 30, fig. 4).

That portion of wall coated by algal calcite is shown (when repolished and re-etched, Pl. 30, fig. 5) to be composed of typical thin stereotheca composed of spherulitic clusters, expanding towards the centre of the corallite and with the axis of the cluster perpendicular to the outer margin of the wall (Pl. 30, fig. 6). The lower part of this micrograph shows a rather large amount of randomly distributed material (apparently organic debris) in the algal coating. Endolithic algae have also apparently bored into the wall of this *Thecosmilia*, so this Triassic coral not only has a perfectly modern skeletal structure but is also associated with modern-looking algae.

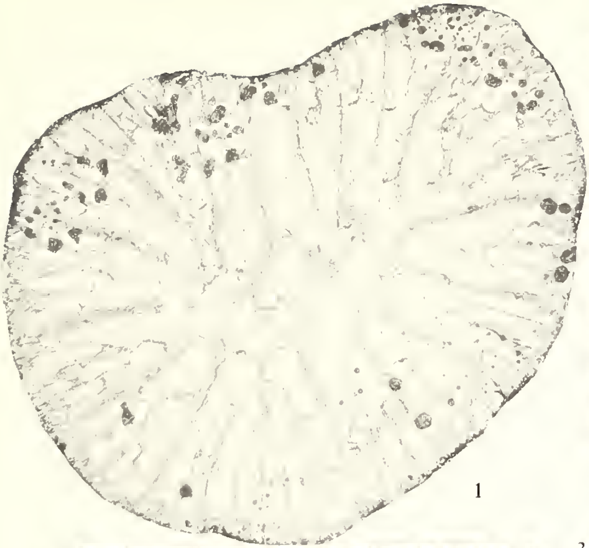
In some septal cross-sections, this specimen of *Thecosmilia* does show slight effects of recrystallization, predicated by James's model and also shown by magnesium content in microprobe traverses. This recrystallization of trabecular centres (Pl. 30, figs. 2 and 3) is most likely reflecting susceptibility to solution of very fine crystallites in trabecular centres.



TEXT-FIG. 3. *Thecosmilia badiotica* (USNM 245274). Composite micrographs showing line of electron microprobe as for text-fig. 2. Here the traverse line begins at the left in a coating of algal calcite, passes into the corallite through the wall, and traverses septa and interseptal carbonate. Note again that trabecular centres are visible in the septa and are also marked by anomalous amounts of MgO and SrO.

EXPLANATION OF PLATE 30

Figs. 1-6. *Thecosmilia badiotica* Volz (USNM 245274). 1, transverse view in thin-section (of specimen about to bud), × 10. 2, scanning electron micrograph (SEM) longitudinal to corallite axis, transverse to septum showing trabecular centres with little alteration of central crystals, × 400. 3, SEM enlargement of centre of septal trabecula from septum in fig. 4, illustrating minor recrystallization of fine aragonite crystallites to calcite, × 2000. 4, SEM transverse to dissepiment with central junction groove on basal surface (arrow), × 400. 5, SEM providing overview of septa and algal material shown in text-fig. 3, after repolishing and re-etching, × 50. 6, SEM enlarging portion of fig. 5, to show theca with crystal clusters and axis of clusters perpendicular to outer surface of wall, coated with algal calcitic mass (arrow at junction). Note also scattered whitish organic debris in algal coating, × 500.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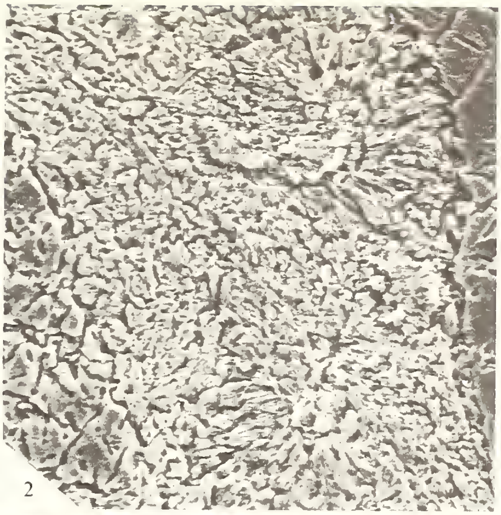
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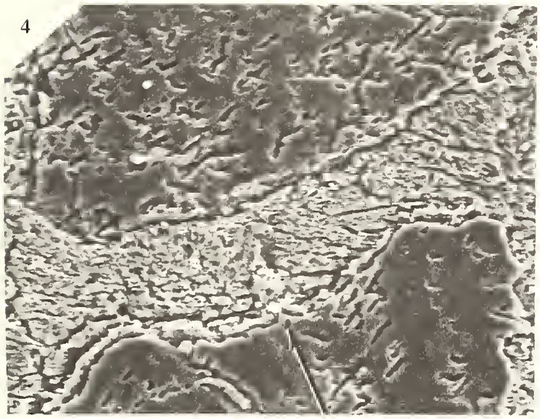

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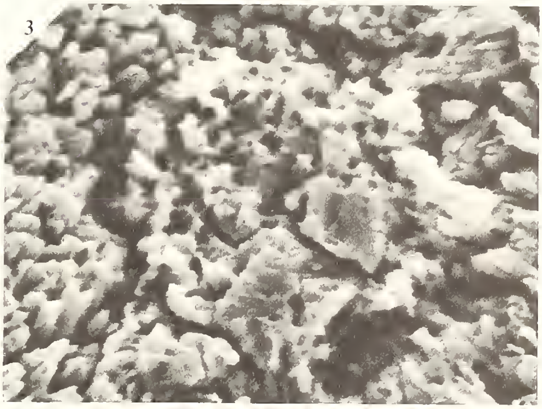

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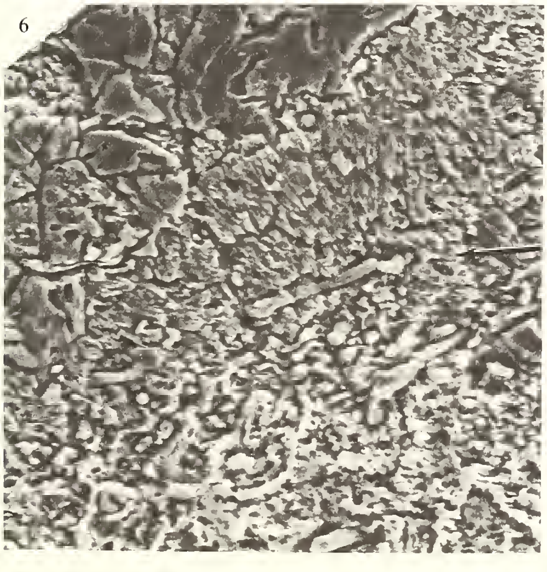

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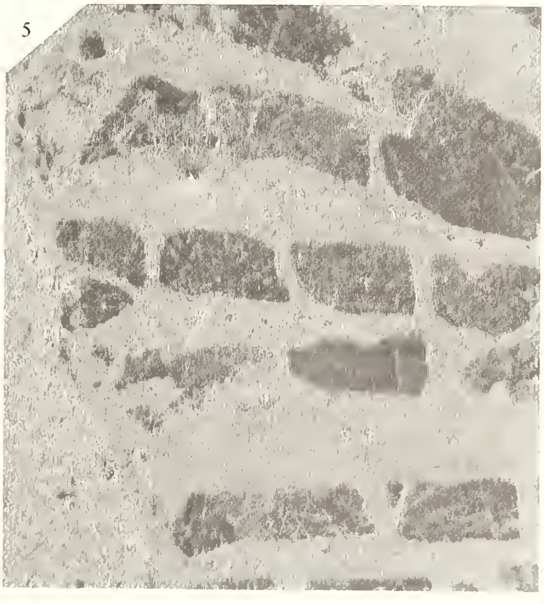

SORAUF, coral structure

Isastraea cf. *I. gumbeli* Laube

Although no chemical analyses have been made on *Isastraea* cf. *I. gumbeli*, some structural studies are presented here which provide further evidence of the modern appearance of these corals. In longitudinal thin-section, the large septal trabeculae are clearly shown, along with some inorganic aragonitic overgrowths on flanks of septa (Pl. 31, fig. 1). In SEMs of polished and etched sections of septa, trabeculae appear to be large, with well-marked centres, and form dentation apparent on the proximal margin of the septa (Pl. 31, fig. 2). Micrographs of dissepiments as cut transversely in a section longitudinal to the corallite axis show two characteristic features, the upward growth of crystals in the main portion of the dissepiments, and the widespread occurrence and modern appearance of endolithic algae (Pl. 31, fig. 3).

PERMIAN CORALS

The Permian corals from Timor have been studied the same way as the Triassic scleractinians, as noted previously. Three genera are reported on, *Polycoelia*, *Timorophyllum*, and *Lophophyllidium*, with the greatest emphasis on the first two.

It is here noted that useful studies could be made on broken sections of *Polycoelia* and *Timorophyllum*, with results comparable to those obtained by study of Recent corals in broken section. This is the first time that such studies have been successful on Palaeozoic corals, and attests to the splendid preservation of these specimens.

Polycoelia angusta Rothpletz

P. angusta is a small, solitary rugose coral characterized by bilateral symmetry, thick stereotheca and septa with the axial ends expanded (Pl. 31, fig. 4). It can be seen in thin-section that the fine structure shows axial ends of the septa inflated by incremented growth, with dark growth lines clearly visible within this part of the septum. Here trabeculae are strongly inclined axially and the main crystallite growth is (at the tip) laterally orientated towards the axis of the corallite (Pl. 31, fig. 5). The zigzag structure is variably developed within the walls of this specimen.

In a microprobe scan line run across five septa and intervening interseptal spar, it is immediately noted that the SrO content counts are at the background level of the

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EXPLANATION OF PLATE 31

Figs. 1–3. *Isastraea* cf. *I. gumbeli* Laube (USNM 245275). 1, longitudinal thin-section of septal trabeculae, slightly oblique to plane of section, showing preservation of what are apparently aragonitic overgrowths on trabeculae (arrow), × 36. 2, SEM longitudinal to septum near crest, illustrating large trabeculae with well-marked centres (arrow) and trabecular denticulations on septal crests, × 400. 3, illustration of transverse section of dissepiment, polished and etched, to show upward growth of crystals and presence of endolithic algae (arrow), × 500.

Figs. 4, 5. *Polycoelia angusta* Rothpletz (G-PMM-B2.399). 4, transverse section of small corallite, with typical symmetry and septa with inflated axial tips, × 10. 5, enlargement of axial end of long septum at right-hand side of fig. 4, here showing fibrous crystal structure and incremental growth lines, plane polarized, × 75.

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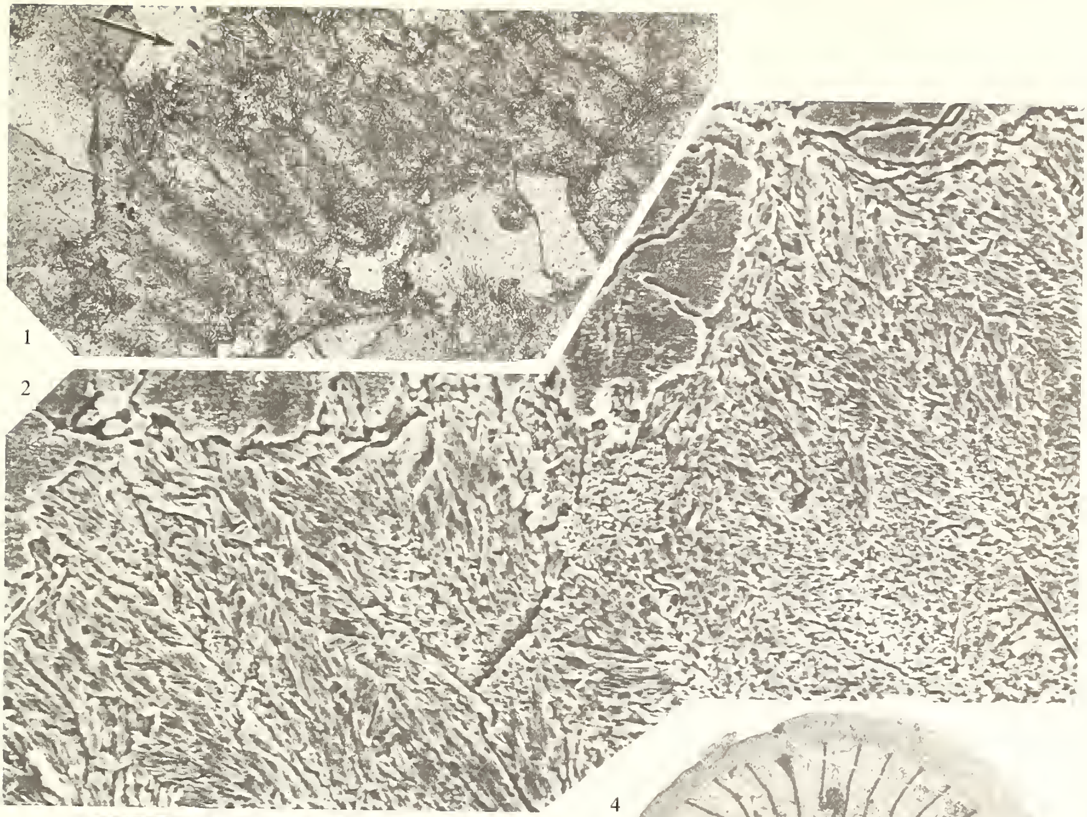

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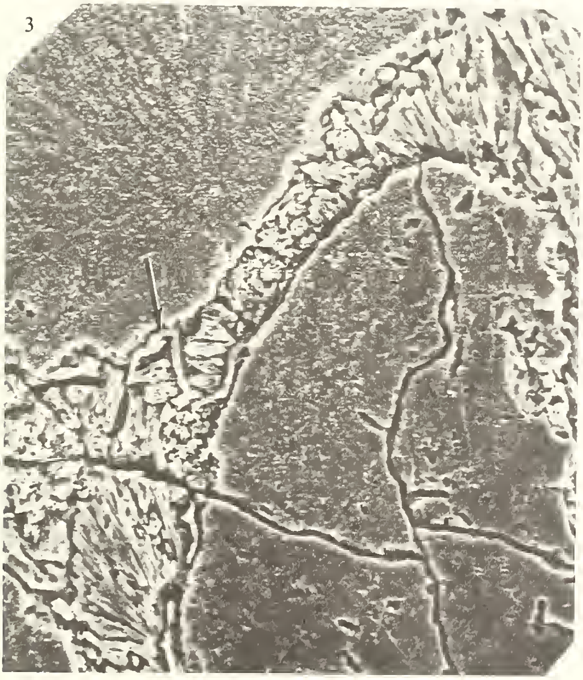

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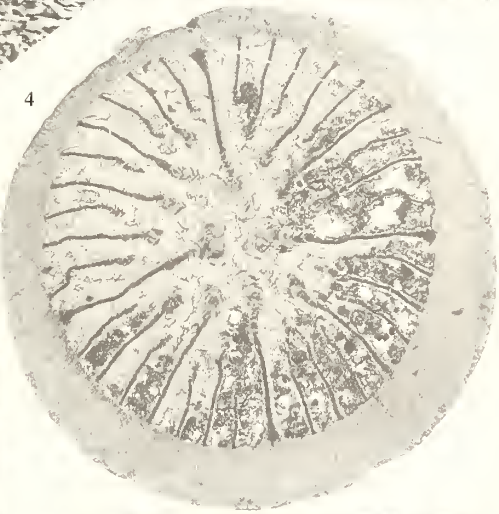

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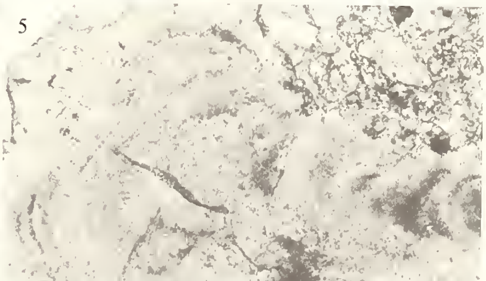
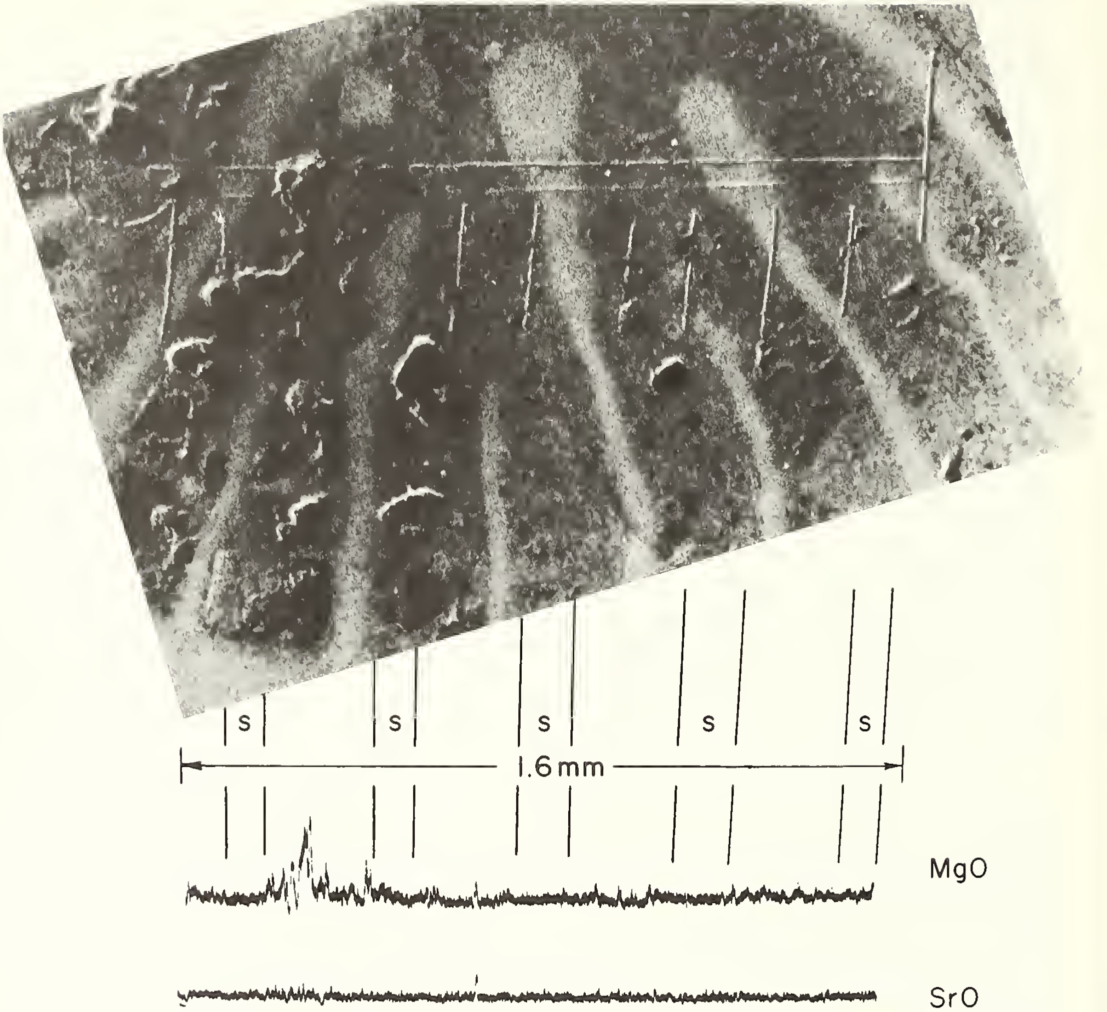


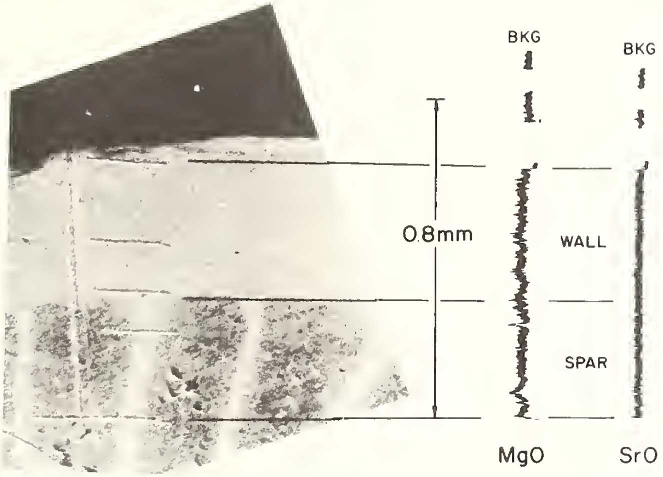
SORAUF, coral structure



TEXT-FIG. 4. *Polycoelia angusta* (G-PMM-B2.399). Composite micrographs of traverse across septa of *Polycoelia* as in text-fig. 2. Note that there exists little or no difference in MgO content between septa and spar. The peak near the left side of the MgO line corresponds with topographic irregularity shown above on the scan line and is apparently a result of the hole at the surface of the sample.

instrument (text-fig. 4), and that the MgO distribution is not markedly different between septa and spar, although the magnesium distribution curve is perhaps somewhat more uniform (fewer pertubations) in some septa. However, as the greatest character in the MgO count is produced by surface irregularities (text-fig. 4), it is entirely possible that the only variations noted in this curve are the result of variation in the perfection of the surface polish. Certainly the minor element content of the calcitic septa is not markedly different from that of the interseptal spar. When these same septa were repolished and re-etched (Pl. 32, fig. 1), the specimen shows the truly magnificent preservation of the septa, with the axial tip of the septum characterized by extremely small crystals, with growth lines visible on the scanning micrograph (Pl. 32, fig. 1).

The wall of the corallite was likewise analysed for minor element distribution by a line of traverse perpendicular to the outer surfaces of the wall (text-fig. 5). Here again, little magnesium is noted and the strontium content is apparently near zero. This analysis of the wall was made specifically to obtain bearing on the so-called zigzag wall structure, present in some of the thick-walled specimens of the Timor fauna, first discussed by Schindewolf (1942, p. 36). This microprobe data is totally inconclusive except to reinforce the opinion that the wall is here similar in composition to the interseptal spar infilling the corallite.



TEXT-FIG. 5. *Polycoelia angusta* (G-PMM-B2.399). Composite of scanning micrograph of outer portion of corallite showing wall, septa, interseptal spar, and scale and traverse line as in text-fig. 2. Note that there is no difference apparent between the MgO content of wall and of spar.

This same specimen, when repolished and more fully etched, illustrates quite well the zigzag appearance of the wall structure seen in transverse section (Pl. 32, fig. 2). However, in the same micrograph can be seen a septum inserted in the wall. The orientation of the crystals within the septum bears no obvious relation to the orientation of crystals within the wall. That this septum is very well preserved is illustrated by its remarkable appearance in the broken section of the tip of the septum (Pl. 32, fig. 3). The crystal structure can be seen just as on the polished and etched section, here not only with divergent crystals but also with remarkably small crystal sizes in the centre of the septum. A broken section of the wall shows the cause of the zigzag structure. This section (Pl. 32, fig. 4) shows a generally transverse section, but a third dimension is also clearly visible. It is in this direction, longitudinal to the corallite, that recrystallization (perhaps coupled with directed pressures) has formed crystals greatly enlarged in the vertical direction, forming large lath-like crystals that are deformed so that when cut in transverse section they clearly show the zigzag form. The very large size of these crystals, apparently recrystallized, lends further credence to the proposed diagenetic origin for this structure (Oekentorp 1974; Sorauf 1977). A view of the septum discussed earlier (Pl. 32, fig. 5) shows that it is fine-grained, with divergent crystals all the way to the junction with the area of recrystallized calcite (the wall), with no apparent continuity of the structure across this boundary. This clearly suggests that the wall has been greatly modified since formed and that the septum has at the same time remained almost totally unchanged.

Timorophyllum wanneri Gerth

T. wanneri is a medium-sized solitary coral (diameter of 1·0–1·2 cm) characterized by a columella which imparts a definite bilateral symmetry to the corallite in transverse section (Pl. 33, fig. 1). The fine structure of the septa as seen in transverse section shows a central dark line with crystallite growth out perpendicularly towards the flanks of the septa. Crystal growth in the walls is likewise perpendicular to the outer surface of the wall, with septa having an inserted appearance into the wall (in this figure, the characteristic is somewhat exaggerated by solution at this boundary). Under higher magnification, the dark line is seen as a line of fine crystals connecting septal trabeculae, also with small crystals in the trabecular centres. This same specimen, analysed for MgO, shows that there is a significantly smaller amount of magnesium in the septa than in the interseptal spar (text-fig. 6) and also that the septa are quite uniform in their composition. The spar is apparently more variable in magnesium distribution, but it is not possible to quantify this, owing to surface irregularities in the polish of this part of the specimen.

Although there is an appreciable difference in composition between septa and spar in this specimen of *Timorophyllum* another equally well-preserved specimen (Pl. 33, fig. 2) does not show this. In this microprobe traverse of this well-preserved septum (text-fig. 7), there is no difference apparent between the septal calcite and the sparry calcite, and the data would seem here to be inconclusive.

EXPLANATION OF PLATE 32

Figs. 1–5. *Polycoelia angusta* Rothpletz (G-PMM-B2.399). All scanning electron micrographs (SEM). 1, enlargement of tip of septum, illustrating fine diverging crystals and visible growth lamellae, × 200. 2, zigzag structure in same wall illustrated in text-fig. 5, here repolished and re-etched. Here, in transverse section, no relation is seen between the structure of the wall and that of the septum (arrow) at right, × 200. 3, transverse view in broken section across septum, illustrating small diverging crystals, just as in polished and etched section (Pl. 32, fig. 1), × 500. 4, broken section of wall with upper portion of micrograph showing transverse section of wall (arrow) but with third dimension illustrating elongation of large crystals in the longitudinal direction, with their junctions providing zigzag structure, × 1000. 5, broken section of wall and dissepiment showing non-congruency of structure at junction of the two (arrow), × 500.

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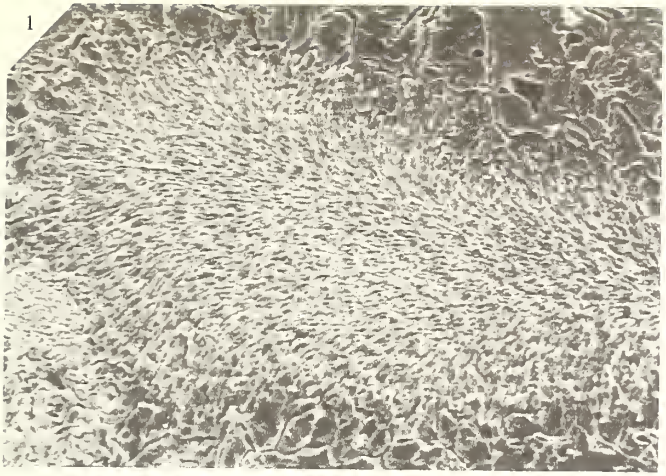

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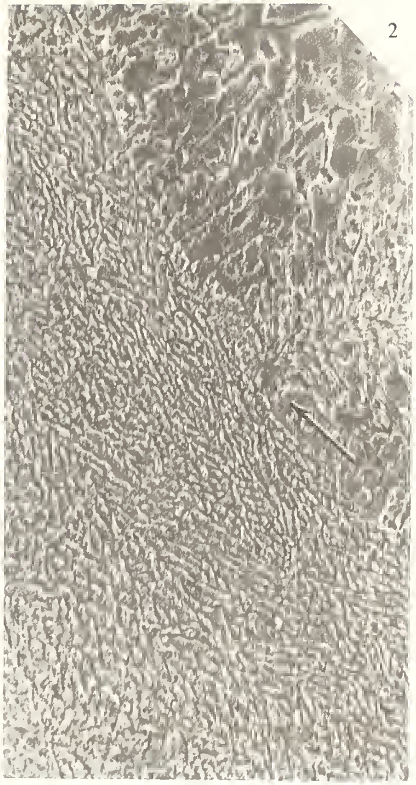

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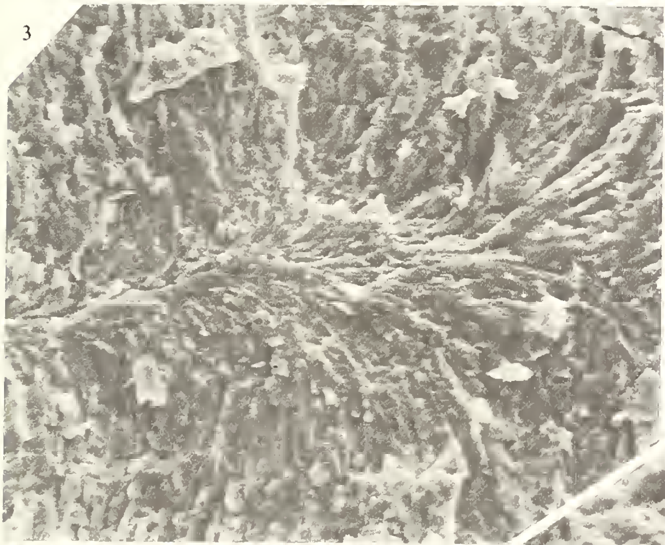

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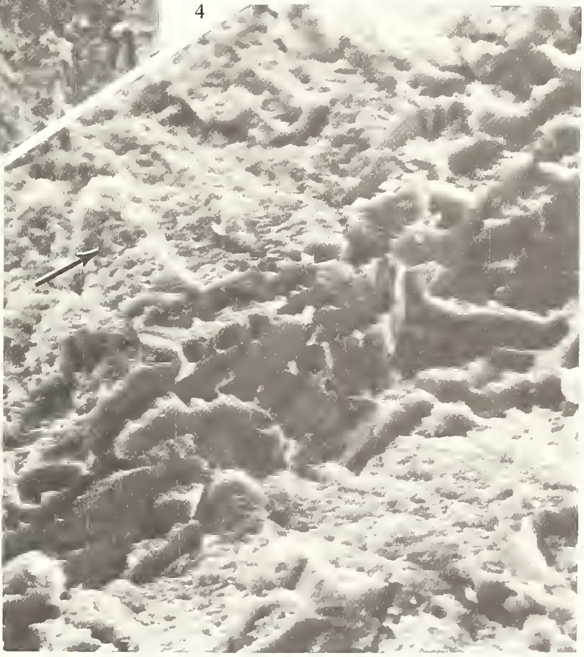

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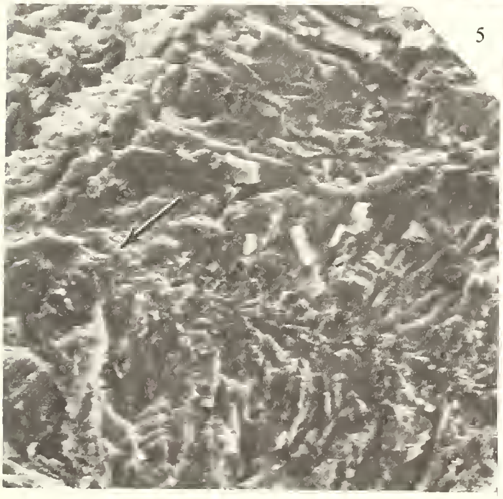
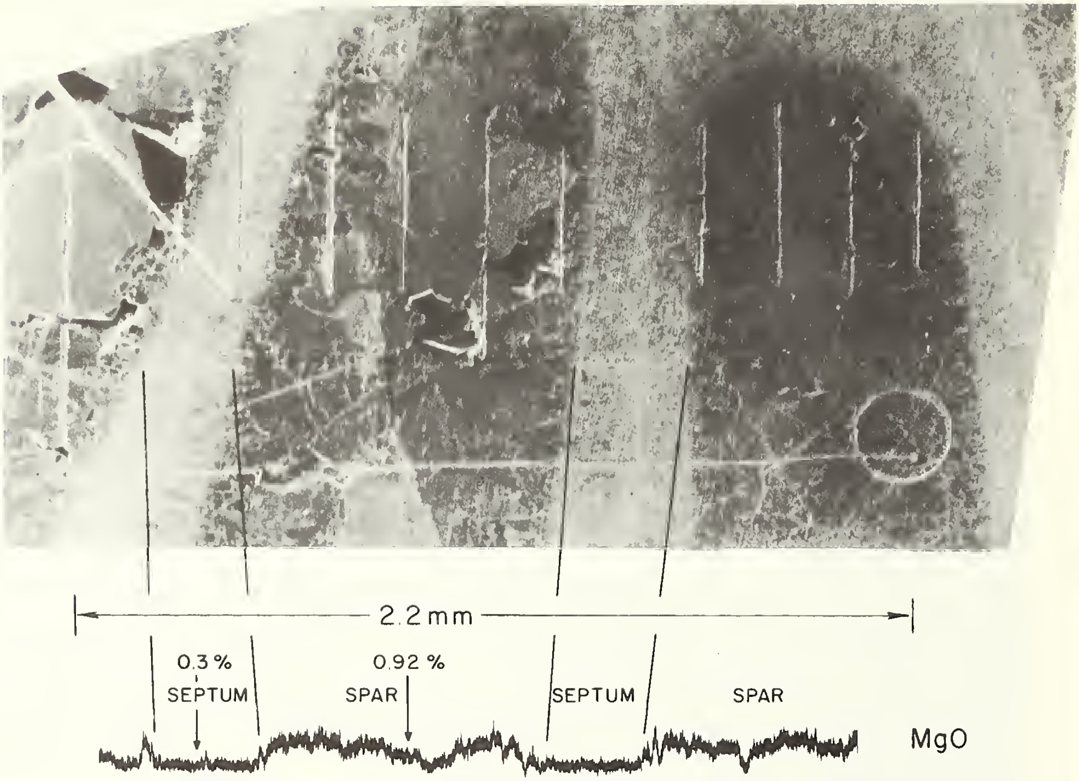


SORAUF, coral structure



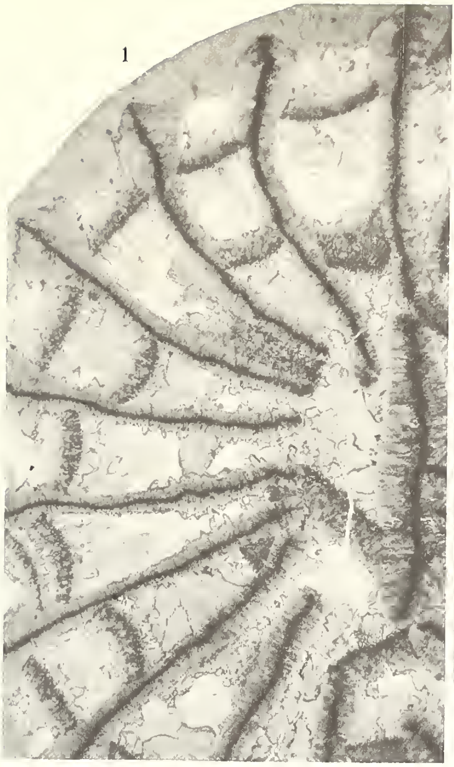
TEXT-FIG. 6. *Timorophyllum wanneri* (G-PMM-B2.400). Composite micrographs illustrating position of microprobe scan line as shown by lines drawn from MgO printout line to trace of scan line after light etching, as for text-fig. 2. Note that septal calcite has a lower MgO content than does interseptal spar. The weight percentages of MgO are approximate only.

EXPLANATION OF PLATE 33

Fig. 1. *Timorophyllum wanneri* Gerth (G-PMM-B2.400). Transverse view of corallite showing columella, symmetry, and central dark line to septa, and crystal growth perpendicular to margins of both wall and septa.

Fig. 2. *Timorophyllum wanneri* Gerth (G-PMM-B2.401). SEM transverse to tip of septum showing very well-delineated septal trabeculae, and crystal overgrowth extending structure, × 400.

Figs. 3–5. *Lophophyllidium spinosum* Martin (G-PMM-B2.402). 3, transverse view illustrating columella and remarkable quartz crystal overgrowths on elongate septa, × 7·5. 4, enlargement of portion of previous view showing acicular quartz crystals and clear centres to septal trabeculae, × 25. 5, SEM of polished and etched transverse section of septum with silicification duplicating radiating crystal structure of septal trabeculae, × 200.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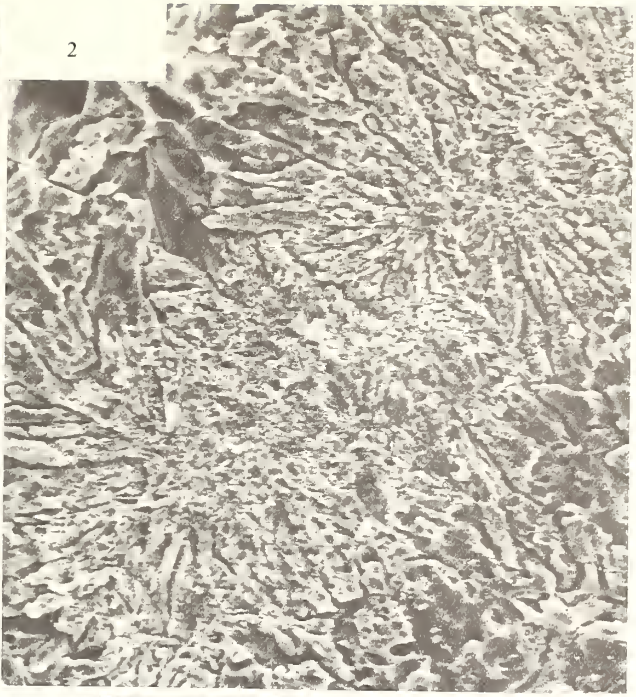
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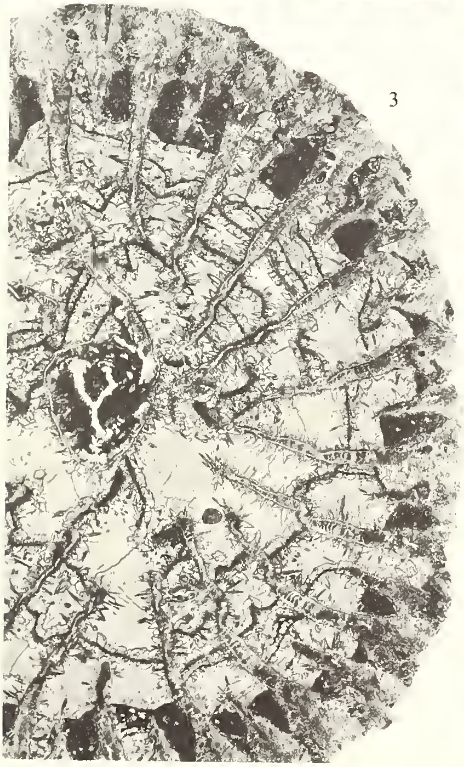
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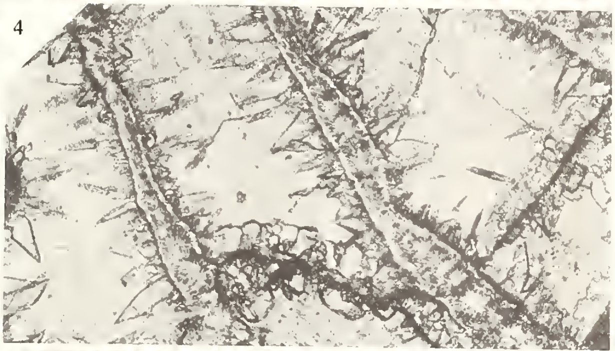
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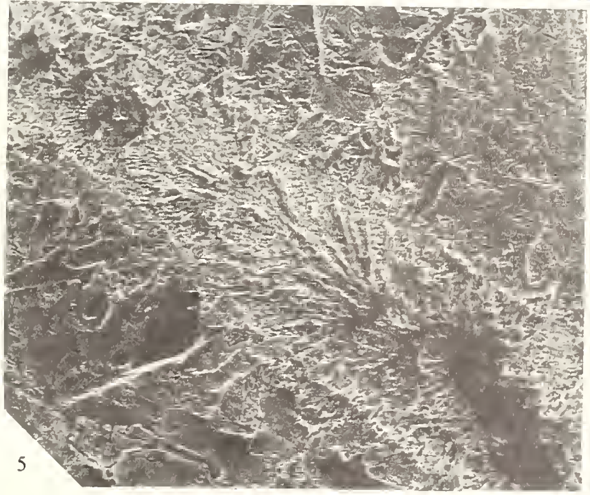
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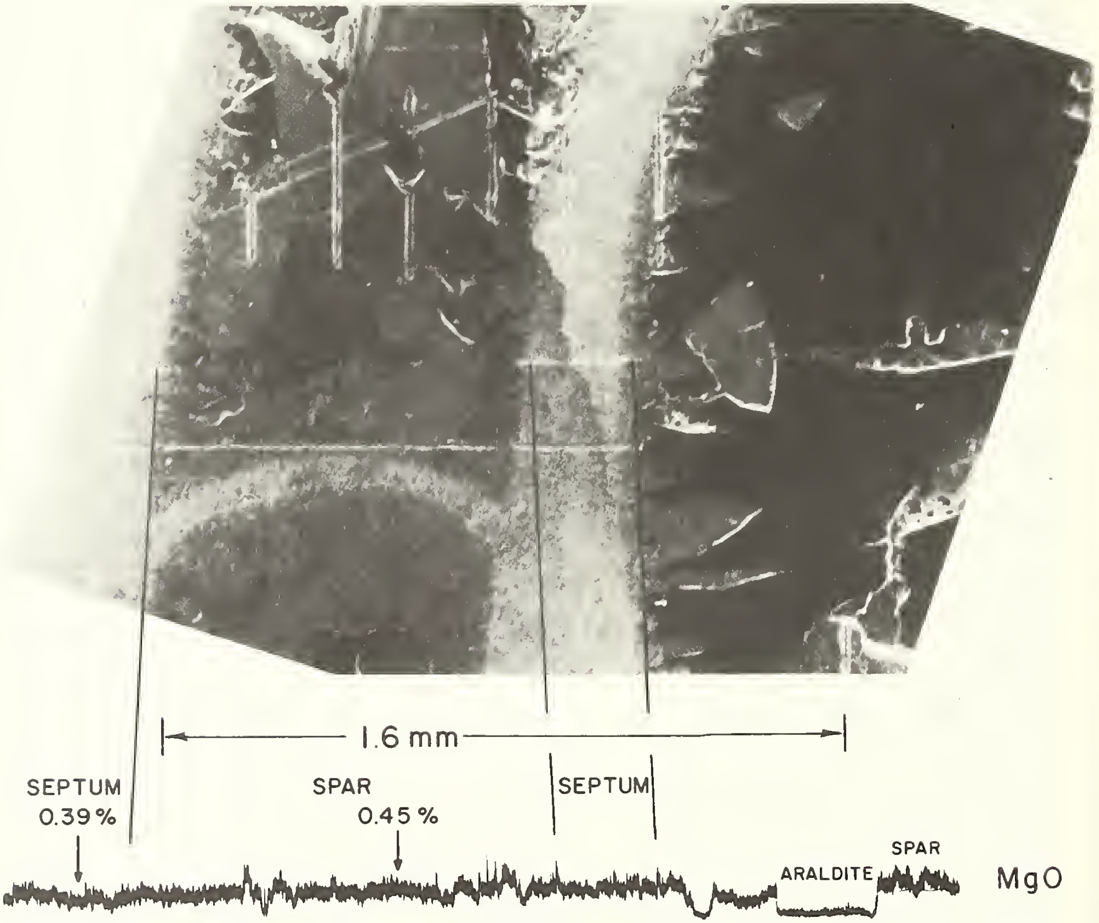
SORAUF, coral structure

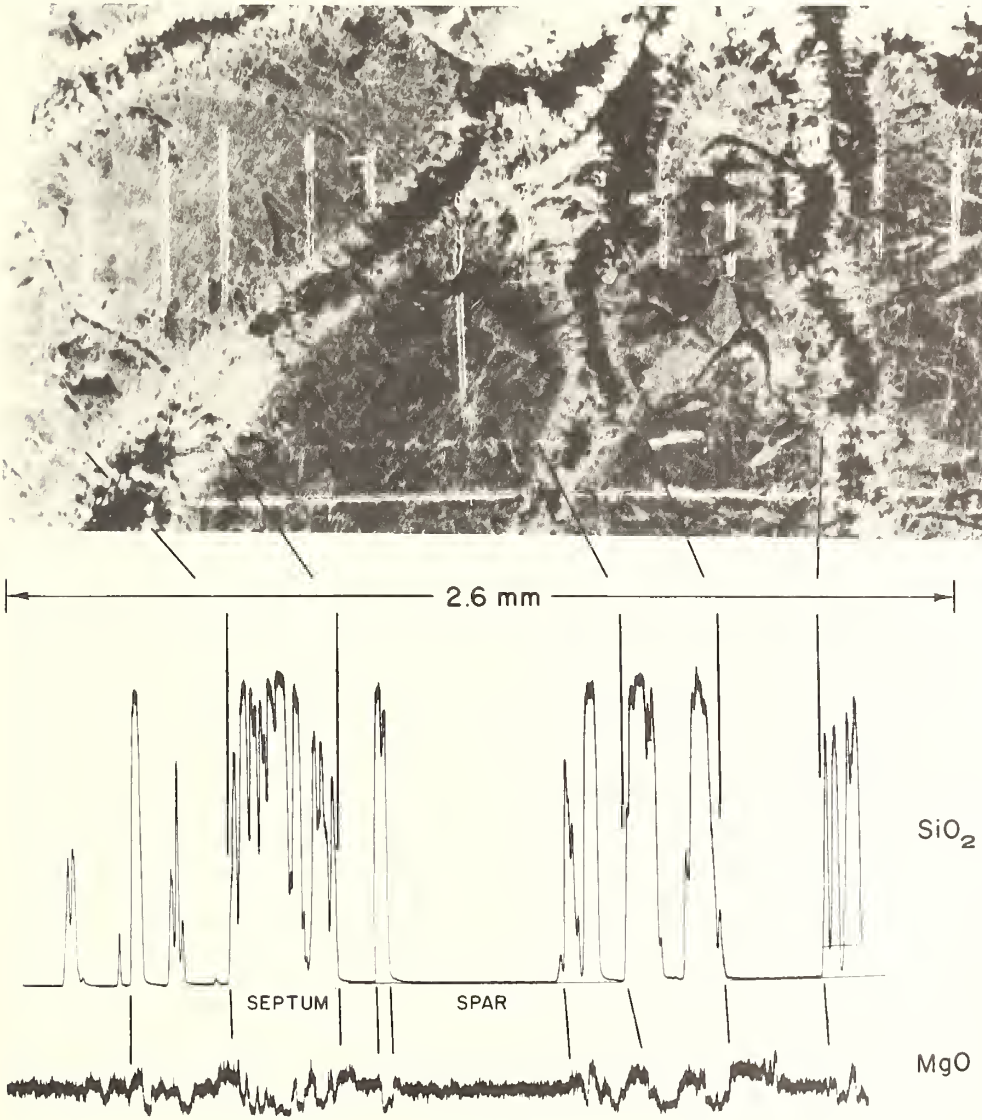
Lophophyllidium spinosum Martin

A single partially silicified specimen of *L. spinosum* was examined for structure and chemistry. This *Lophophyllidium* is characterized by long thin septa and prominent columella (Pl. 33, fig. 3). Although not immediately apparent, this specimen is partially altered (Pl. 33, fig. 4), although the fine structure of the septa has not been greatly altered: trabecular centres can be seen rather clearly in this photomicrograph. A microprobe traverse across several septa does indeed show major amounts of silica, especially in the trabecular centre at the left side of this micrograph (text-fig. 8). Repolishing and re-etching of this septum shows clearly the preferential silicification of the trabecular centres (Pl. 33, fig. 5) and indeed, preferential silicification of crystals radiating from the centres. This is a peculiarity which has not previously been reported



TEXT-FIG. 7. *Timorophyllum wanneri* (G-PMM-B2.401). Composite micrographs illustrating path of MgO scan line, as in text-fig. 2, after a light etch. Septa are here very much the same as interseptal spar with regards to magnesium content.

from other corals, either rugosans or scleractinians. The evidence is slight, and further data should be collected before making a more detailed hypothesis. I suspect, however, that the silica is replacing unrecrystallized carbonate and duplicating biogenic structures. This type of incipient silicification (or other diagenetic processes) starts at centres of trabeculae, just as calcitization of modern aragonitic corals begins at the centres of trabeculae where the crystals are smallest.



TEXT-FIG. 8. *Lophophyllidium spinosum* (G-PMM-B2.402). Composite micrographs to show position of microprobe scan lines as in text-fig. 2. Note that a close correspondence is seen between occurrence of silica and magnesium. It can also be noted here that silica is replacing trabecular centres of septa preferentially.

CONCLUSIONS

Late Triassic aragonitic corals are among the first-known scleractinians; their structure and minor element content is very like that of Recent corals (as shown for strontium by Montanaro Gallitelli, Morandi and Pirani 1973). Diffusion, if actually a factor affecting minor element distribution in carbonates, has apparently been of equal importance in lowering relative amounts of strontium and magnesium, not only in skeletal aragonite, but also in interseptal calcite spar.

Permian corals from Timor are among the best-preserved rugosans known. This fact, noted in thin-sections and in SEMs of polished and etched sections, is reflected to a remarkable degree in the septal structures and trabeculae noted in broken sections of both *Polycoelia* and *Timorophyllum*. The fact that crystal sizes noted in broken sections of trabeculae are not much different than those seen in trabeculae of modern corals is considered convincing evidence that little recrystallization has taken place in the skeletal carbonate.

Minor element analysis shows that negligible amounts of strontium and magnesium are present. This is in contrast with some data (Richter 1972; Sorauf 1977) that rugose corals had an elevated magnesium content in skeletal calcite. In the Timor specimens there is no apparent, consistent difference between composition of the spar and the composition of the skeleton.

The sole identifiable diagenetic fabric ('structure') noted is the zigzag seen in the wall of *P. angusta*. This wall makes an abrupt and discontinuous contact with the septa, which are still exceptionally well preserved. The diagenetic structure was recognizable in part because of the very large size of the crystals relative to those within the septal trabeculae, reinforcing the hypothesis that septal calcite is not recrystallized in these specimens.

Early stages of silicification of *L. spinosum* show a concentration of silica in centres of septal trabeculae, with this replacement process replicating the septal microstructure rather faithfully. This suggests that the silica was replacing unrecrystallized calcite. It is also important to note that the region of replacement is the same as in the vadose calcitic replacement of Pleistocene scleractinians. In both cases, replacement is first in the very fine-grained grained centres of trabeculae.

Diagenetic structures such as zigzag features are (to me) unknown in any post-Palaeozoic corals. I would infer that they are diagenetic structures developed in biogenic calcite but not in aragonite replaced by calcite. The remarkable preservation of skeletal structures in calcitic Permian corals at the electron microscopic scale, and the completely different minor element chemistry suggest that the Rugosa originally had a skeleton of calcite, just as the Scleractinia have always had a skeleton of aragonite. This is likely to be the result of biological factors (protein chemistry, enzymal activity), rather than a reflection of external environment.

Acknowledgements. I am indebted to Professors P. de Bethune and R. Conil respectively, who during the fall of 1975 graciously made me welcome in the electron microprobe facility and the Palaeontology Laboratory at the University of Louvain, Louvain-la-Neuve, Belgium. Special thanks are due to Mr. Jacques Wautier, who provided the necessary expertise for the microprobe analyses reported here, and to Mr. H. H. Tsien for general assistance during my stay in Belgium. Scanning electron microscopy was done with the instrument in the Department of Geological Sciences and Environmental Studies at the State

University of New York, Binghampton. Photographic expertise was provided by Mr. David Tuttle of this institution. Loan of specimens from the Friedrich Wilhelm University of Münster (Westphalia) was kindly arranged by Dr. Klemens Oekentorp.

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BIOGEOGRAPHY OF PERMIAN ECTOPROCT BRYOZOA

by JUNE R. P. ROSS

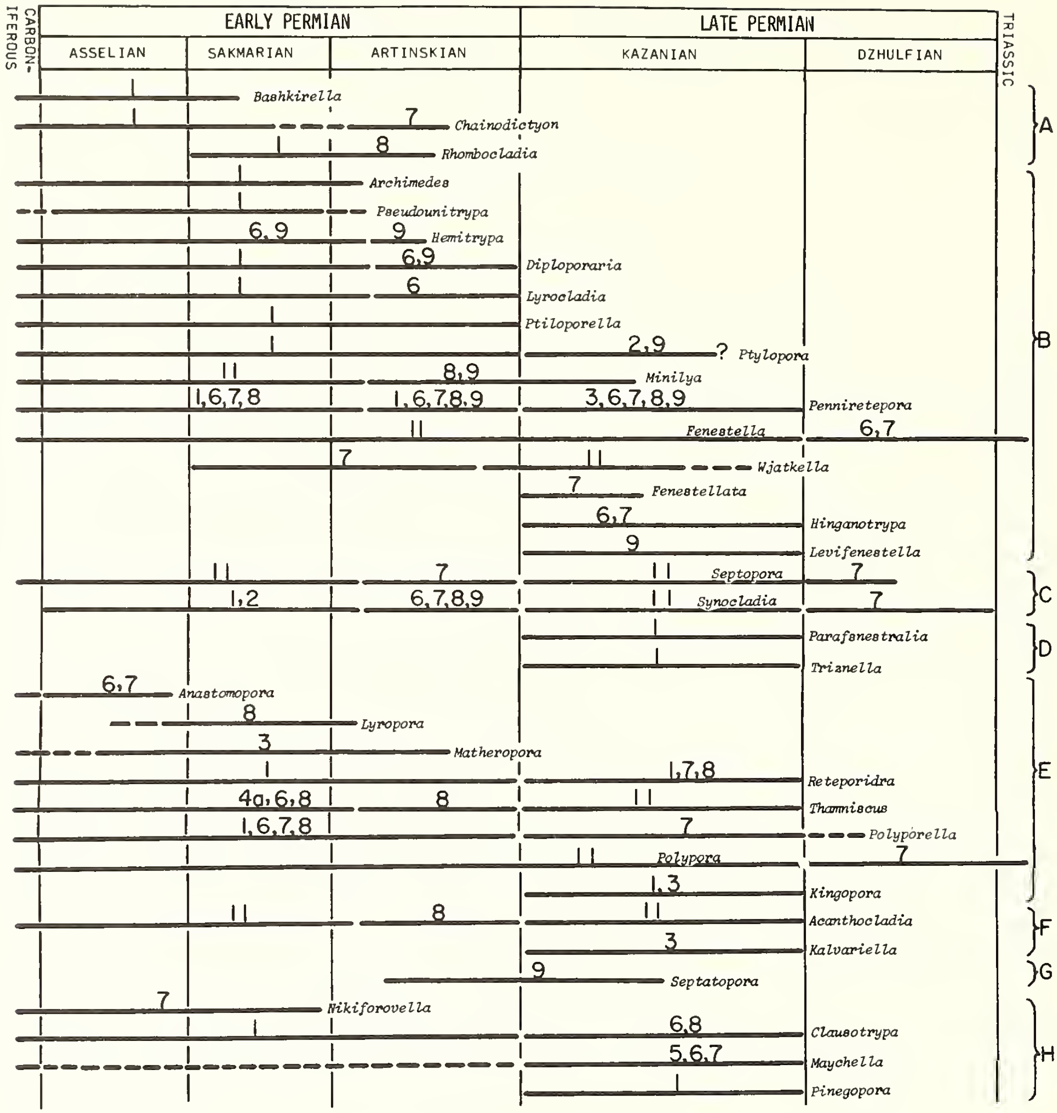
ABSTRACT. Earliest Permian (Asselian and early Sakmarian) ectoprocts were widespread, included many lineages of Carboniferous origin, and had a large number of cosmopolitan genera. Marked geographic differences in their generic diversity suggest that physical parameters, such as temperature, were important factors in controlling ectoproct distributions. Late Sakmarian and Artinskian ectoprocts show a number of distribution patterns, as well as the beginning of a clearly defined Tethyan fauna with a number of endemic genera. During the Artinskian, Tethyan genera have greater dispersal so that certain areas, such as Australia and Pakistan, contain a number of Tethyan genera, whereas other areas, such as the Uralian and Franklinian regions, received only a few immigrant Tethyan genera.

By the early part of the Kazanian, ectoprocts are strongly provincial with Tethyan faunas having both high diversity and endemism and non-Tethyan faunas having low diversity. Ectoprocts from Zechstein strata have unusually low diversity, perhaps because of major fluctuations in temperature or salinity, and Australian ectoprocts are also less diverse at this time. Dzhulfian ectoprocts are greatly reduced in generic diversity, geographic distribution, and in total numbers because many lineages become extinct near the middle of the Late Permian. Most ectoprocts of the late Dzhulfian are remnants of Tethyan endemic lineages and only a few genera survive into the earliest Triassic before becoming extinct.

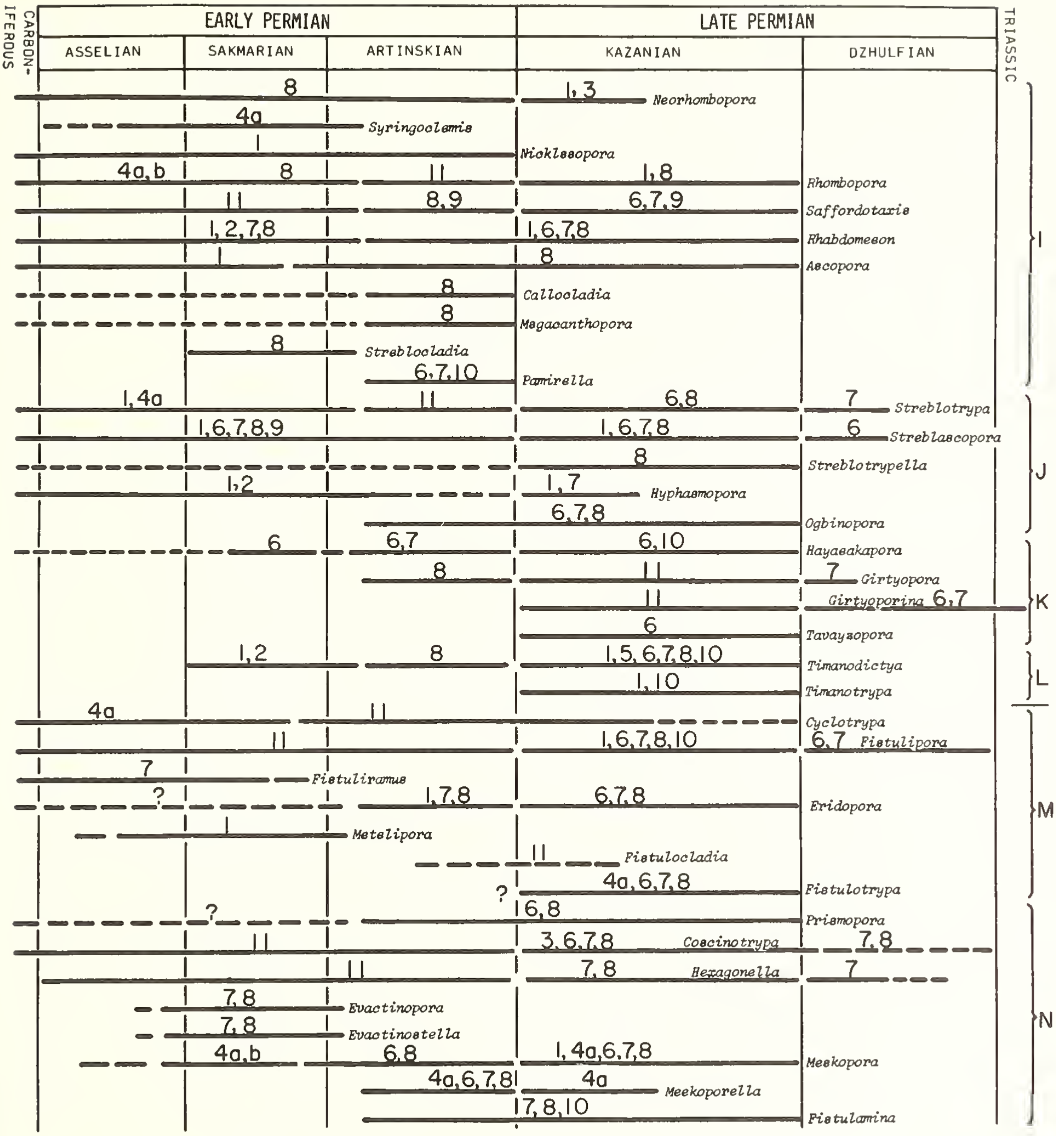
ECTOPROCTS are significant elements in many Permian marine faunas and environments. Cystoporates and cryptostomes are commonly dominant, whereas trepostomes are far less abundant. Text-figs. 1–3 show the Permian range and geographic distributions of ectoproct genera arranged by families. This classification in general closely follows those given by Morozova (1970) and Gorjunova (1975) and has been updated and modified on the basis of additional published and unpublished information on particular genera. Cystoporates, having 25 genera in 6 families, gradually increase in abundance and diversity through the early and middle parts of the Permian and become restricted in distribution in the later part of the Permian. Cryptostomes, having 58 genera in 12 families, developed in a similar pattern to the cystoporates in the Permian. Trepostomes, having 19 genera in 6 families and uncertain family assignment for 2 of these genera, only modestly increased their diversification through the Permian until late Kazanian time when drastic reduction and extinction in numbers of genera occurred. The stratigraphic terminology and correlation of sections in North America, the Russian Platform, and two Tethyan regions (Transcaucasus, and Darvas and Pamir), as used in this paper, are shown in text-fig. 4.

Ectoprocts are among a large number of marine benthic invertebrates that came close to extinction near the end of Permian time. For most invertebrate groups, phylogeny, geographic distribution, and dispersal history are incompletely known or have been only partially examined for the Permian Period. As a result the details of the faunal histories of different invertebrate groups are difficult to relate to each other and to the many physical events which may be deduced from the geologic record. This study summarizes the available data for ectoprocts in terms of their patterns of geographic distribution, their dispersal, and the changes in these patterns during the Permian.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 341–356.]

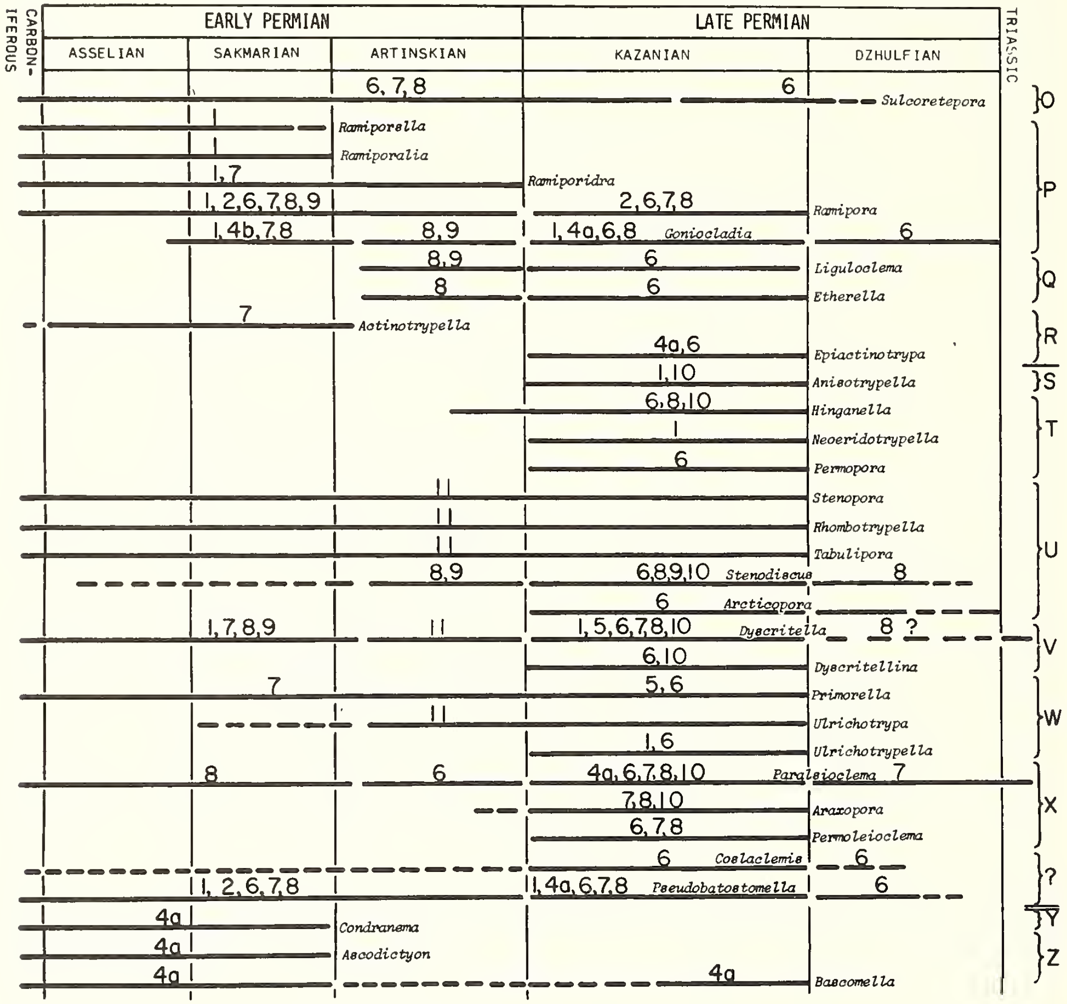


TEXT-FIG. 1. Stratigraphic range and geographical distribution of Permian ectoproct genera; class Stenolaemata, order Cryptostomata: families A, Phylloporinidae, B, Fenestellidae, C, Septoporidae, D, Fenestraliidae, E, Polyporidae, F, Acanthocladiidae, G, Septatoporidae, and H, Nikiforovellidae. Geographical regions are: 1, Russian Platform and Uralian Sea; 2, Franklinian Sea and adjacent shelf; 3, Zechstein Sea; 4, North America, southern part and near-by areas (4a, west Texas and midcontinent; 4b, Andean Sea); 5, parts of northern Siberia and adjacent regions, U.S.S.R.; 6, northern Tethys including the Maritime Territory and Kabarovsk region of U.S.S.R., Japan, and western parts of North American Cordillera; 7, central Tethys including Transcaucasus, Darvas, Pamir, Tibet, Mongolia, and south-west China; 8, southern Tethys including parts of Afghanistan, Salt Range of Pakistan, Western Australia, Malaya, and Thailand; 9, Tasman Geosyncline; 10, North American Cordillera, eastern part; and 11, cosmopolitan distribution. See also text-fig. 5.



TEXT-FIG. 2. Stratigraphic range and geographic distribution of Permian ectoproct genera; order Cryptostomata (continued): families I, Rhabdomesidae, J, Hyphasmoporidae, K, Girtyoporidae, and L, Timanodictyidae. Order Cystoporata: families M, Fistuliporidae, N, Hexagonellidae. See text-figs. 1 and 5 for key to numbered geographical regions.

Information from this group of organisms should contribute to a more thorough understanding of late Palaeozoic biogeographical relationships and may have important implications concerning the time, and the nature, of changes in marine connections between different areas. It may help in elucidating changes in characteristics of ocean currents, and changes in local and world climates and in temperature gradients.



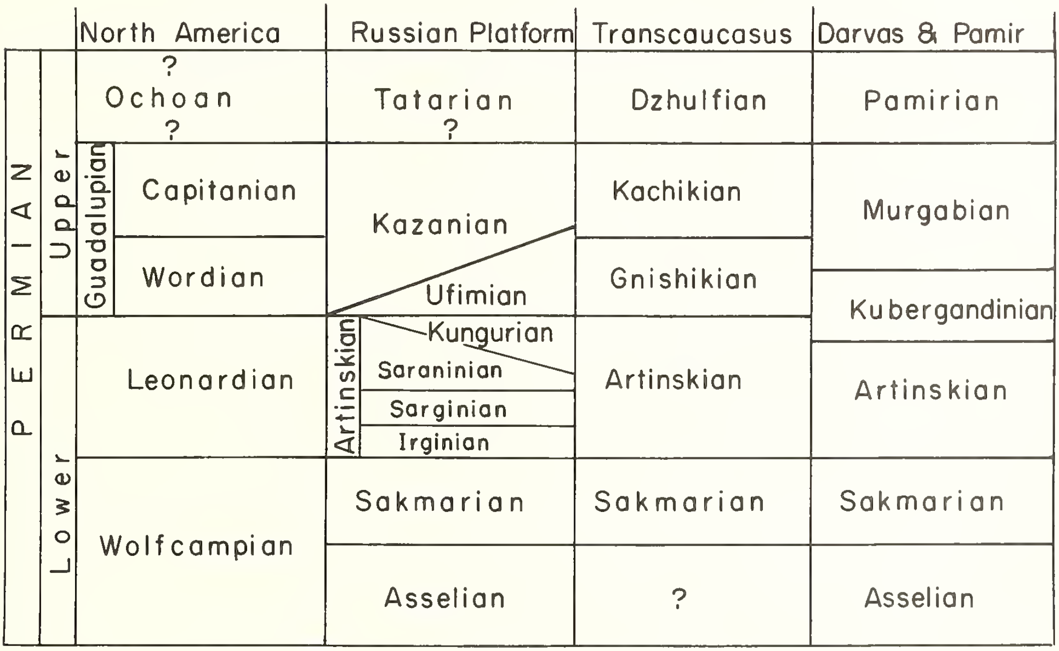
TEXT-FIG. 3. Stratigraphic range and geographical distribution of Permian ectoproct genera; order Cystoporata (continued): families O, Sulcoreteporidae, P, Goniocladiidae, Q, Etherellidae, and R, Actinotrypidae. Order Trepostomata: families S, Anisotrypidae, T, Eridotrypellidae, U, Stenoporidae, V, Dyscritellidae, W, Ulrichotrypellidae, X, Araxoporidae, and (?) *Incertae sedis*. Class Gymnolaemata, order Ctenostomata: families Y, Vinellidae and Z, Ascodictyidae. See text-figs. 1 and 5 for key to numbered geographical regions.

PALAEOGEOGRAPHIC DISTRIBUTION

Information on phyletic evolution and biogeographic patterns for Permian ectoprocts, as with other invertebrate groups, is far more complete for certain regions of the world and particular rock sequences than for others. In some areas large gaps exist in our knowledge of the composition of ectoproct faunas. Extensive faunas are known from the Russian Platform, Ural Mountain region, Transcaucasus, Pamir and Darvas region, Maritime Territory of the U.S.S.R., Kabarovsk, and Far East regions of the U.S.S.R. Newly described faunas are available from China, Tibet, Japan, Thailand, and Malaya. Described ectoproct faunas from western and eastern Australian basins provide considerable data, as do early studies on faunas from Timor. Only sketchy information is available from the Salt Range, Pakistan, and adjoining areas of India and Kashmir, and also for the Carnic Alps. In the mid 1960s ectoprocts from the German Zechstein strata were re-examined and some information for England and north-east Greenland and Spitsbergen is available. Permian faunas of North America and South America remain very incompletely studied. These various faunas are assigned to ten palaeogeographic regions in reconstructing the ectoproct distributional patterns (text-fig. 5). The following discussion summarizes major ectoproct faunal features of these regions.

Russian Platform and Uralian Sea

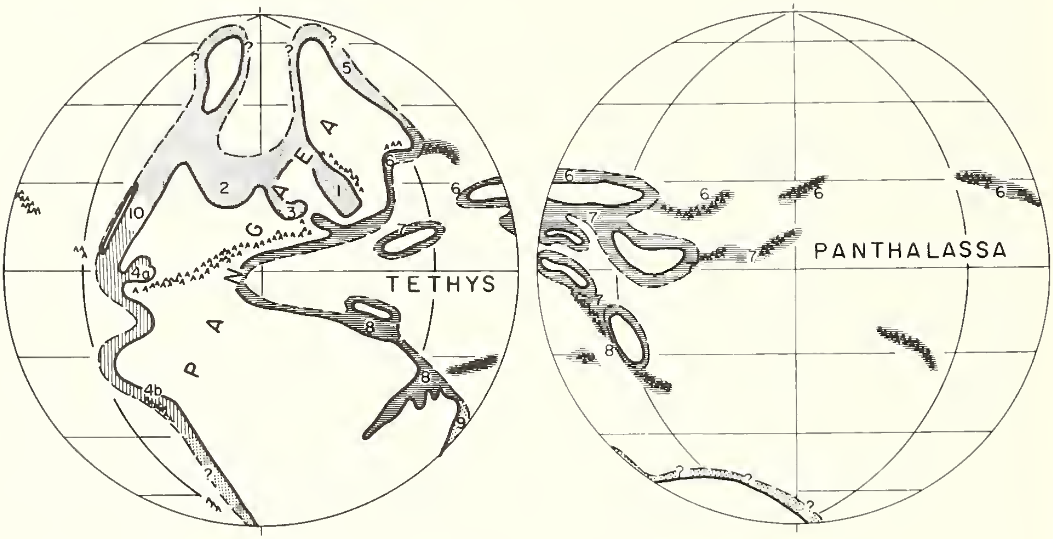
On the Russian Platform and adjacent shelf areas rich ectoproct faunas were a continuation of Carboniferous faunas and extend up into the later part of the



			North America	Russian Platform		Transcaucasus	Darvas & Pamir
PERMIAN	Upper		? Ochoan ?	Tatarian ?		Dzhulfian	Pamirian
		Guadalupian	Capitanian	Kazanian		Kachikian	Murgabian
			Wordian	Ufimian		Gnishikian	Kubergandinian
	Lower		Leonardian	Artinskian	Kungurian	Artinskian	
					Saraninian		Artinskian
					Sarginian		
					Irginian		
			Wolfcampian	Sakmarian		Sakmarian	Sakmarian
				Asselian		?	Asselian

TEXT-FIG. 4. Permian correlation chart comparing stratigraphic nomenclature in North America, Russian Platform, and two Tethyan regions (Transcaucasus, and Darvas and Pamir).

Kazanian (Nikiforova 1939; Trizna 1950; Shulga-Nesterenko 1952; Trizna and Klautsan 1961; and Morozova 1970). In the Asselian and Sakmarian fenestrate cryptostomes of the families Fenestellidae and Polyporidae were dominent members of the hydractinoid reefs and adjacent shelf biota. In addition, the cryptostomes *Ascopora*, *Nicklesopora*, *Streblotrypa*, *Acanthocladia*, and *Timanodictya*, the stenoporid trepostome *Rhombotrypella*, and the cystoporates, *Hexagonella*, *Fistulipora*, and *Ramipora*, were also part of this rich fauna. Although only sixteen genera are listed for the Sakmarian of this region, the fauna is rich and diverse in species.



TEXT-FIG. 5. Palaeogeographic reconstruction for the early part of the Late Permian. Numbers refer to the following regions: 1, Russian Platform and Uralian Sea; 2, Franklinian Sea and adjacent shelf; 3, Zechstein Sea; 4, North America, southern part (4a), and Andean Sea (4b); 5, parts of northern Siberia and adjacent regions, U.S.S.R.; 6, northern Tethys including the Maritime Territory and Kabarovsk region of U.S.S.R., Japan, and western parts of North American Cordillera; 7, central Tethys including Transcaucasus, Darvas, Pamir, Tibet, Mongolia, and south-west China; 8, southern Tethys including parts of Afghanistan, Salt Range of Pakistan, Western Australia, Malaya, and Thailand; 9, Tasman Geosyncline; and 10, North American Cordillera, eastern part.

During Early Artinskian (Irginian) time, generic diversity remained high and ectoprocts were abundant in reef limestones and bedded limestone shelf facies (Trizna and Klautsan 1961). Only a few Sakmarian species persisted into the Artinskian so that the majority of species are new. The greatest number of new species belong to *Fenestella* and *Polypora*. *Rhombotrypella*, *Penniretepora*, *Clausotrypa*, and *Hexagonella* also flourished. However, *Timanodictya*, *Reteporidra*, *Lyrocladia*, *Ascopora*, and *Nicklesopora* were less abundant than they were in the Sakmarian. Goniocladiids, such as *Goniocladia*, became a significant part of the fauna in the early and middle part of Artinskian time and new genera, such as *Ptylopora* and *Ptiloporella*, first appear in Early Artinskian time.

During Middle Artinskian (Sarginian) time, generic diversity continued to be high and the greatly varied lithofacies of reef and intrareef environments were highly suited for ectoprocts. About half of the species are new and the remainder continue from Sakmarian or early Artinskian ectoproct faunas. The trepostomes *Pseudobatostomella* and *Stenopora*, the fistuliporid cystoporate *Eridopora*, and some rhabdomesid cryptostomes are significant parts of these ectoproct assemblages. Species of *Fenestella* and *Polypora* remained important in the fauna.

Before the end of Artinskian time, generic diversity decreased markedly in ectoprocts, apparently as a result of changes in the Uralian Geosyncline and on the Russian Platform due to tectonic movements (Nalivkin 1973). *Fenestella*, *Polypora*, *Rhombotrypella*, *Pseudobatostomella*, and *Streblotrypa* have new species assemblages and are well represented. *Paraleioclema* and *Tabulipora* are additions to the assemblages. Both *Clausotrypa* and *Hexagonella*, however, disappear before the end of the Artinskian.

In Kazanian time (Morozova 1970) the generic diversity gradient for ectoprocts increases from the southern part of the Uralian Sea north and westward towards the Arkhangel region. Eleven genera are present in the southern part of the Uralian Sea in the region of Tatarian A.S.S.R., whereas in the north, twenty-six genera are present. Genera that are well represented in all parts of this Uralian Sea include the trepostomes *Pseudobatostomella*, *Dyscritella*, *Rhombotrypella*, and *Tabulipora*, and the cryptostomes *Wjatkella*, *Fenestella*, *Streblascopora*, *Pinegopora*, *Parafenestralia*, and *Triznella*. In the northern region these genera are joined by six other genera, the trepostomes *Ulrichotrypella* and *Anisotrypella*, the cystoporates *Goniocladia* and *Meekopora*, and the cryptostomes *Timanotrypa* and *Girtyoporina*. No ectoprocts are reported in younger units of the Late Permian on the Russian Platform and adjacent regions.

Franklinian Sea, Barents Shelf, and adjacent shelves

Although not well known, ectoprocts from this region, which stretches from Novaya Zemlya to Spitsbergen, Greenland, and the Canadian Arctic Islands, have affinities with faunas of the Russian Platform and Uralian Sea. In north-east Greenland, Sakmarian strata contain the trepostomes *Rhombotrypella*, *Stenopora*, and *Tabulipora* and the cryptostomes *Polypora*, *Fenestella*, and *Timanodictya* (Ross and Ross 1962). A sparse Early Permian fauna from Novaya Zemlya has *Pseudobatostomella*?, *Fenestella*, *Ramipora*, and *Hyphasmopora* (Nikiforova 1936). From Spitsbergen, an Upper Permian fauna of probable Kazanian age has *Fenestella*, *Polypora*, *Ptylopora*, *Septopora*, *Stenopora*, *Tabulipora*, and *Ramipora* (Nikiforova 1936; Malecki 1968).

Zechstein Sea (Late Permian) of England, Germany, Poland, and southern Baltic region

In western Europe, fenestrate cryptostomes dominate the Late Permian faunas but have low generic diversity. In this region the polyporid *Kingopora* and *Fenestella* have a wide distribution and the fauna may also include the cryptostomes *Thamniscus*, *Acanthocladia*, *Penniretepora*, and *Synocladia*, the trepostome *Stenopora*, and the hexagonellid cystoporate *Coscinotrypa* (Dreyer 1961).

North America, southern part

Faunas from this region are poorly known but assemblages have been described from the midcontinent region of the United States (Moore and Dudley 1944) and Texas (Girty 1908; Morozova 1966, 1970). In the midcontinent region (Nebraska, Kansas, Oklahoma) cryptostomes are abundant in strata of Wolfcampian age and include *Fenestella*, *Polypora*, *Septopora*, *Thamniscus*, *Streblotrypa*, *Rhombopora*, and *Syringoclemis*. The Wolfcampian of Nebraska contains the fistuliporid cystoporate *Cyclotrypa* and in Kansas the hexagonellid cystoporate *Meekopora*. These cystoporates are present also in the Leonardian with *Meekoporella* and *Fistulipora* and all four genera extend into the early Guadalupian (Wordian). In the Guadalupian the cystoporates *Goniocladia* and *Epiactinotrypa* also appear. Early Guadalupian cryptostomes are characterized by increased diversity with *Acanthocladia*, *Fenestella*, *Polypora*, *Thamniscus*, *Girtyopora*, and *Girtyoporina*. The trepostomes are *Pseudobatostomella*?, *Stenopora*, and *Paraleioclema*? Younger Guadalupian (Capitanian) faunas contain the cystoporates *Fistulipora* and *Goniocladia*, the cryptostomes *Acanthocladia*, *Fenestella*, and *Girtyoporina*, and the trepostome *Paraleioclema*.

Andean Sea

Two Early Permian (Wolfcampian) faunas in southern Peru contain the cystoporates *Goniocladia* and *Meekopora*, the cryptostomes *Acanthocladia*, *Fenestella*, *Polypora*, *Septopora*, and *Rhombopora* (Chronic 1953).

Parts of northern Siberia and adjacent regions, U.S.S.R.

A late Permian fauna from the Kolyma and Omolon massifs and adjacent regions includes an abundance of cryptostomes, such as *Fenestella*, *Wjatkella*, *Maychella*, *Polypora*, *Synocladia*, and *Timanodictya*, the cystoporate *Fistulipora*, and the trepostomes *Dyscritella* and *Primorella* (Nekhoroshev 1935, 1959; Morozova 1970).

Northern Tethyan Sea

This region includes Japan, the Maritime Territory of the U.S.S.R., Kabarovsk region, and possibly parts of the north-eastern Siberian region of the U.S.S.R. In Japan, ectoproct faunas are abundant in a number of depositional basins and range through most of the Permian (Sakagami 1970). Asselian and Sakmarian ectoprocts (Zone of *Pseudoschwagerina*) include the cystoporates *Sulcoretepora*, *Fistulipora*, and *Coscinotrypa*, the trepostomes *Pseudobatostomella*, *Stenopora*, and *Tabulipora*, and a great many cryptostomes, such as *Anastomopora*, *Fenestella*, *Penniretepora*, *Polypora*, *Thamniscus*, *Hayasakapora*, and *Streblascopora*. Artinskian ectoprocts (Zone of *Parafusulina*) include *Fistulipora*, *Pseudobatostomella*, *Stenopora*, *Fenestella*, *Penniretepora*, *Hayasakapora*, and *Streblascopora*, which range up from the zone below, and hexagonellid cystoporates *Meekopora*, *Meekoporella*, and *Prismopora*, which show considerable diversity. In the Zone of *Neoschwagerina* (Early Guadalupian as correlated by Ross and Nassichuk 1970), many genera range up from the Zone of *Parafusulina* and additional genera include the hexagonellid *Fistulamina*, the cryptostomes *Saffordotaxis* and *Septopora*, and the trepostome *Ulrichotrypella*. In the Japanese succession the youngest ectoprocts occur in the Zone of *Yabeina–Lepidolina* (Late Guadalupian to Early Dzhulfian) and include many cystoporates, such as

Coscinotrypa, *Fistulipora*, *Goniocladia*, *Meekopora*, *Prismopora*, *Ramipora*, and *Sulcoretepora*. Cryptostomes are represented by *Clausotrypa*, *Rhabdomeson*, *Septopora*, and *Synocladia* and trepostomes remain sparse.

In the Maritime Territory and Kabarovsk region of the U.S.S.R., Permian strata are structurally complex and have an abundant ectoproct fauna (Nikitina, Kiseleva, and Burago 1970). The Early Permian part of these faunas is poorly known. Strata of Kazanian age contain *Coscinotrypa*, *Fenestella*, *Polypora*, *Dyscritella*, *Paraleioclema*, and *Permoleioclema* and, from the upper part of the Zone of *Yabeina*, Morozova (1970) lists thirty genera, eighteen of which occurred in both the Maritime Territory and Kabarovsk region. Both areas contain the cystoporates *Fistulamina* and *Fistulipora*, the trepostomes *Dyscritella*, *Hinganella*, *Ulrichotrypella*, *Stenodiscus*?, *Tabulipora*, *Paraleioclema*, and abundant cryptostomes, such as *Clausotrypa*, *Fenestella*, *Polypora*, *Septopora*, *Girtyoporina*, *Girtyopora*, *Rhabdomeson*, *Streblascopora*, and *Maychella*.

Central Tethyan Sea

This region includes the Transcaucasus, Darvas, Pamir, part of Afghanistan, Tibet, Mongolia, and south-west China.

In the Transcaucasus region, cryptostomes dominate the Late Permian fauna (Morozova 1970). The ectoprocts in the Gnishikian (Early Guadalupian) include the cryptostomes *Fenestella*, *Polypora*, *Septopora*, *Rhabdomeson*, *Streblascopora*, and *Ogbinopora*, the cystoporates *Fistulipora*, *Cyclotrypa*, *Hexagonella*, and *Sulcoretepora*, and the trepostomes *Paraleioclema* and *Araxopora*. In the Kachikian (later Guadalupian) only the trepostome *Araxopora* is reported. The Dzhulfian has the cryptostomes *Polypora*, *Septopora*, *Synocladia*, *Streblotrypa*, and *Girtyoporina*, and the cystoporate *Fistulipora*.

In the Darvas and Pamir region ectoproct faunas range from Asselian into Pamirian strata (Gorjunova 1975). In the Early Permian ectoprocts are abundant, whereas Late Permian ectoprocts are sparse. In south-west Darvas, Asselian and Sakmarian ectoprocts include the cystoporates, *Actinotrypella*, *Fistulipora*, *Goniocladia*, *Ramiporida*, and *Sulcoretepora*, the trepostomes *Rhombotrypella* and *Primorella*, and the cryptostomes *Rhabdomeson* and *Streblascopora*. Artinskian ectoprocts are less diverse and include the cystoporates *Cyclotrypa*, *Eridopora*, *Fistulipora*, and *Hexagonella*. Sakmarian deposits in south-east Pamir have biostromes of the cryptostome *Nikiforovella*. Artinskian deposits have a more diverse fauna including the cystoporates *Fistulamina* and *Ramiporidra*, the trepostomes *Dyscritella* and *Rhombotrypella*, and abundant cryptostomes *Pamirella* and *Streblascopora*.

In south-west Darvas the lower part of the Upper Permian has no recorded ectoprocts and, in the upper part of the Upper Permian, only the cystoporate *Fistulipora* is thus far reported. In central Pamir Late Permian ectoprocts include the cystoporates *Eridopora* and *Fistulipora* and the cryptostome *Ogbinopora*. In south-east Pamir the cystoporate *Hexagonella* and the trepostome *Araxopora* are reported from the Murgabian.

In central eastern China, in the Yangshin Series, the Lower Permian Chihsia Limestone has the cosmopolitan genera *Fenestella*, *Polypora*, *Septopora*, and *Fistulipora* (Loo 1958). The first three of these genera, as well as *Acanthocladia*, *Dyscritella*, and *Stenopora*, occur also in the Upper Permian Maokou Limestone in the

Yangshin Series. The succeeding Loping Series contains *Fistulipora*, *Polypora*, *Septopora*, *Penniretepora*, *Synocladia*, *Pseudobatostomella*, and *Paraleioclema*. The Jisu Honguer Limestone of Inner Mongolia has a fauna which is similar to that of the Maokou Limestone. However, the fauna also contains the cryptostomes *Streblascopora*, *Maychella*, *Rhabdomeson*, *Girtyopora*, and *Girtyoporina*, the cystoporates *Fistulamina* and *Hexagonella*, and the trepostomes *Tabulipora* and *Paraleioclema* (Grabau 1931; Morozova 1970).

Southern Tethyan Sea

This region includes central eastern Afghanistan, the Salt Range of Pakistan, Thailand, Malaya, Western Australia, and Timor.

In central eastern Afghanistan, ectoprocts are abundant in Sakmarian to Kazanian strata (Termier and Termier 1971). Sakmarian and Artinskian faunas have many polyporids and fenestellids, such as *Polypora* (*Pustulopora*), *Polypora* (*Paucipora*), *Fenestella*, and *Minilya*. Other cryptostomes are *Rhabdomeson*, *Rhombopora*, *Saffordotaxis*, and *Septopora*. The cystoporates include *Cyclotrypa*, *Goniocladia*, *Meekopora*, and *Sulcoretepora*. The relatively sparse trepostomes include *Dyscritella*, *Rhombotrypella*, and *Tabulipora*. Several genera, including *Rhombotrypella* and the above-mentioned four cystoporates, extend up into the Kubergandinian. The cryptostomes *Ascopora*, *Streblascopora*, *Septopora*, and *Acanthocladia* also appear in the Kubergandinian. In the Murgabian, *Tabulipora* reappears and the cystoporates include *Coscinotrypa*, *Goniocladia*, and *Hexagonella*, and the cryptostomes are *Streblascopora*, *Rhabdomeson*, *Thamniscus*, and *Reteporidra*.

In the Salt Range of Pakistan, Early Permian (Artinskian) ectoproct faunal assemblages have the cystoporates *Fistulipora* and *Hexagonella*, the trepostomes *Stenodiscus* and *Stenopora*, and the cryptostomes *Fenestella*, *Polypora*, *Acanthocladia*, *Thamniscus*, *Rhombopora*, and *Girtyopora*; not a markedly diverse fauna. In the Late Permian the two cystoporates, *Fistulipora* and *Hexagonella*, are joined by *Goniocladia* and the cryptostomes *Polypora*, *Synocladia*, and *Rhombopora* (Waagen and Pichl 1885; Waagen and Wentzel 1886).

In Thailand Late Sakmarian to Late Artinskian ectoproct faunas have many cystoporates, including *Fistulipora*, *Coscinotrypa*, *Goniocladia*, *Hexagonella*, *Liguloclema*, *Sulcoretepora*, and *Ramipora*, many cryptostomes, including *Acanthocladia*, *Fenestella*, *Polypora*, *Thamniscus*, *Penniretepora*, *Rhabdomeson*, *Ascopora*, *Streblascopora*, *Streblotrypa*?, *Rhombopora*, *Ogbinopora*, and *Timanodictya*?, and the trepostomes *Dyscritella* and *Leioclema*? (Sakagami 1970, 1976). Malaya has a distinctive Guadalupian fauna having *Clausotrypa*, *Araxopora*, *Pseudobatostomella*, *Paraleioclema*, and *Fenestella* (Sakagami 1970, 1976).

In the western part of Australia the Fitzroy trough of the Canning Basin and the Carnarvon Basin (Crockford 1951, 1957; Ross 1963) have Sakmarian ectoproct assemblages containing the cystoporates *Evactinostella*, *Fistulipora*, and *Hexagonella*, the cryptostomes *Streblascopora*, *Fenestella*, *Lyropora*, and *Polypora*, and the trepostomes *Dyscritella*, *Stenopora*, and *Paraleioclema*. Artinskian faunas show much greater diversity with the addition of the cystoporates *Prismopora*, *Eridopora*, *Etherella*, *Goniocladia*, *Liguloclema*, *Fistulamina*, *Evactinopora*, and *Ramipora*, and the cryptostomes *Acanthocladia*, *Septopora*, *Synocladia*, *Minilya*, *Saffordotaxis*, *Rhabdomeson*, *Megacanthopora*?, *Callocladia*?, *Rhombocladia*, *Streblotrypa*, and *Streblocladia*. In the Bonaparte Gulf Basin, strata of probable early Late Permian age contain a sparse fauna of *Fistulipora*, *Ramipora*, *Streblotrypa*, and *Rhombopora*. In the Fitzroy trough, Upper Permian strata of Tatarian age have an ectoproct assemblage with *Dyscritella* and *Stenodiscus*.

Not all ectoproct faunas described from Timor (Bassler 1929) are assignable to stratigraphically identified units. Those faunas which are placed stratigraphically include faunas of Early Permian and Late Permian ages. The Bitauni Beds (Artinskian) have a sparse fauna comprised of the cystoporate *Fistulipora*, the cryptostomes *Fenestella*, *Rhombopora*, and *Streblascopora*, and the trepostomes *Hinganella* and *Ulrichotrypa*. In the Basleo Beds (early Late Permian) cystoporates became more abundant and include *Eridopora*, *Fistulotrypa*, *Fistulipora*, *Goniocladia*, and *Hexagonella* and occur with the trepostome *Hinganella* and the cryptostomes *Streblascopora* and *Fenestella*. The overlying Amarassi Beds have a sparse fauna consisting of *Clausotrypa*, *Fenestella*, *Fistulipora*, and *Stenopora*. Younger strata, of probable Late Kazanian age, contain the two cryptostomes *Streblotrypella* and *Rhabdomeson*.

Tasman Geosyncline (eastern Australia)

Permian ectoproct faunas in the northern part of the Tasman Geosyncline have a pattern of diversity similar to that of Western Australia. Sakmarian faunas of the Bowen Basin and Springsure Shelf, Queensland (Wass 1969), are sparse and contain *Fenestella* and *Polypora*. In Artinskian faunas, cystoporates and cryptostomes are more abundant and include *Liguloclema*, *Goniocladia*, *Fistulipora*, *Ramipora*, *Diploporaria*, *Penniretepora*, *Polypora*, *Minilya*, *Saffordotaxis*, *Rhombopora*, and *Streblascopora*. The trepostomes are *Dyscritella*, *Stenodiscus*, and *Stenopora*. The Late Permian (Kazanian) fauna has the cryptostomes *Fenestella*, *Polypora*, *Septatopora*, *Levifenestella*, *Penniretepora*, *Ptylopora*, and *Saffordotaxis*, and the trepostomes *Paraleioclema*?, *Stenodiscus*, and *Stenopora*.

In the southern part of the Tasman Geosyncline (Sydney Basin of New South Wales), the Early Permian (Sakmarian) faunas are restricted and include only *Dyscritella* and *Stenopora*. In slightly younger (Artinskian) strata species diversity increases markedly, particularly in the genus *Stenopora*. Also, additional genera are found in this part of the sequence and include *Fenestella*, *Minilya*, *Polypora*, *Rhombopora*, and *Pseudobatostomella*? Strata of the same age in Tasmania also show great species diversity in *Stenopora* and, in addition, also contain *Stenodiscus* and *Hemitrypa*?

North American Cordilleran Geosyncline and adjacent shelf

A published abstract on the Guadalupian faunas from this region (Gilmour and Snyder 1976) indicates that the generic composition of assemblages from north-eastern Washington, north-eastern Nevada, and central Wyoming has similarities with the faunas of the Russian Platform, Maritime Territory of the U.S.S.R., and Japan. *Fenestella*, *Polypora*, *Timanotrypa*, *Fistulipora*, *Anisotrypella Paraleioclema*, and *Stenodiscus* occur in all three regions. Other genera such as *Wjaktella*, *Girtyopora*, *Girtyoporina*, *Hayasakapora*, *Pamirella*, *Timanodictya*, *Cyclotrypa*, *Hinganella*, *Stenopora*, *Araxopora*, *Rhombotrypella*, and *Ulrichotrypa* are also present only in parts of the North American Cordillera. This generic grouping suggests a mixing of Tethyan and non-Tethyan elements.

Africa

Permian ectoprocts occur in scattered localities in Africa, including Egypt and Tunisia, but little faunal data are published. Fenestellid fragments and the trepostome *Dyscritella* were found in the lower part of the Dwyka Tillite in Namibia (South West Africa) (Wass 1972). Associated bivalves indicate a Kazanian age for these beds.

SUMMARY OF DISTRIBUTIONS

Many cystoporate genera during much of the Early Permian are widespread, particularly among the fistuliporids (*Fistulipora*, *Cyclotrypa*), the hexagonellids (*Hexagonella*, *Coscinotrypa*, *Meekopora*), and the goniocladiids (*Goniocladia*, *Ramipora*). During the early part of the Late Permian (Kazanian), some of these (*Cyclotrypa*, *Goniocladia*, *Meekopora*, and *Ramipora*) continue to have a widespread distribution. Other cystoporates, such as the hexagonellids *Evactinopora*, *Evactinostella*, *Fistulamina*, *Prismopora*, and the sulcoreteporid *Sulcoretepora*, form a distinctive part of many Early Permian Tethyan faunas. In Late Permian Tethyan assemblages the fistuliporid *Fistulotrypa*, the hexagonellids *Fistulamina* and *Prismopora*, and the sulcoreteporid *Sulcoretepora* are common.

Trepostomes also are generally either cosmopolitan or Tethyan. *Stenopora*, *Rhombotrypella*, *Tabulipora*, and possibly *Pseudobatostomella* are cosmopolitan genera that range through the Early and into the Late Permian. Genera restricted to Tethyan regions include *Paraleioclema* in the Early and Late Permian and *Araxopora*, *Arcticopora*, *Dyscritellina*, *Permocleioclema*, *Permopora*, and *Primorella* in the Late Permian. A number of genera, such as *Dyscritella*, are widely distributed in the Uralian and Tethyan regions early in the Permian, but become distinctive members of the Tethyan region by Late Permian.

Cryptostomes have different patterns of distribution compared to cystoporates and trepostomes and, because they are more abundant and more widely distributed, they are a more useful group for delineating faunal regions. The fenestellids *Fenestella* and *Penniretepora* and the polyporid *Polypora* appear to be cosmopolitan from the Asselian through the Kazanian. The septoporid *Septopora* is cosmopolitan during the Sakmarian, appears to be restricted to the Tethyan Seas during the Artinskian, and is cosmopolitan again during the Kazanian. The septoporid *Synocladia* first appears in the Franklinian Sea and gradually becomes cosmopolitan by the Early Kazanian. The Uralian Sea region has the distinctive fenestellid genera *Ptylopora* and *Ptiloporella* during the Early Permian and *Parafenestralia* and *Triznella* in the Late Permian. Some cryptostomes display a bipolar distribution in the Early Permian, such as the septoporid *Synocladia* and the fenestellid *Diploporaria*, both of which occur in the Uralian Sea and the Tasman Geosyncline. Several genera, such as the timanodictyid *Timanodictya* and the rhabdomesid *Ascopora*, dispersed from the Uralian Sea into the Tethyan Seas during the Early Permian. Other genera, such as the nikiforovellid

Clausotrypa, are in the Uralian Sea in the Early Permian and in the Tethyan Seas by the Late Permian. However, other genera appear restricted to the Tethyan Seas during the Permian, such as the fenestellid *Hinganotrypa*, the polyporid *Lyropora*, the nikiforovellid *Nikiforovella*, the rhabdomesid *Pamirella*, the girtyoporids *Hayasakapora* and *Tavayzopora*, and the hyphasmoporid *Ogbinopora*.

CONCLUSIONS

The world distribution of Permian ectoproct genera and families shows that the faunas of the Tethyan region are the most diverse and that many genera are restricted to that region. This suggests that Tethyan ectoproct faunal assemblages most likely inhabited warm, probably tropical, water when viewed in conjunction with associated faunas. In the early part of the Early Permian (Asselian, Early Sakmarian), the Uralian and Tethyan Seas had a large number of genera in common suggesting that these two seas were interconnected and their respective temperature or environmental conditions were similar, but not identical. At about this time, the ectoproct assemblages in southwestern Africa, India, Pakistan, and Australia were much reduced in number of genera and families and are associated with glacial deposits. This indicates that these ectoprocts are adapted to cool water, and the low diversity in associated faunas tends to confirm this interpretation.

In the middle and later parts of the Early Permian, a number of changes take place in ectoproct distributions which become progressively more pronounced before the end of the Early Permian. The Tethyan ectoprocts become increasingly more diverse and much of the generic evolution appears centred in one or more parts of that large region. New genera appear in the Uralian Sea, but relatively few disperse into the Tethyan region, so that most of the genera and species lineages become endemic to the Uralian and Franklinian Seas along the north margins of the European and North American continents. By the end of the Early Permian, the Uralian Sea reached an unusual set of environmental conditions that greatly reduced its marine fauna to a few groups, including some ectoprocts, which apparently were adapted to fairly wide ranges in salinity and temperatures. This is suggested by the presence of evaporites, limited associated faunas, and interstratified nonmarine beds. Direct marine connections between the Uralian Sea and the Tethys were probably terminated in the middle part of the Early Permian. The Pakistan and Australian ectoprocts also become increasingly diverse during the middle and later parts of the Early Permian suggesting a rapid warming of those seas. Ectoprocts in these two areas are closely related to each other and to other, more normal, Tethyan assemblages. Although a number of typical Tethyan fossil groups, such as fusulinaceans, some corals, brachiopods, and cephalopods, are not well represented, there are enough similarities to suggest that a southern Tethyan fauna existed which included the portion of the fauna that was able to adapt or disperse in slightly cooler water. The similarity of some of these marginal southern Tethyan faunas to those of the Early Artinskian of the Uralian Sea further suggests that the Uralian Sea was cooler than the typical Tethys. The Tethys during the middle and later parts of the Early Permian appears to have been a broad region (text-fig. 5) and the distribution of Permian ectoprocts suggests that the present-day configuration of the Tethyan faunal belt is the result of three or more tropical to subtropical subregions that have been structurally displaced against one another in post-Palaeozoic time (Monger and Ross 1971; Ross 1976).

In the early part of the Late Permian ectoprocts continued to have much the same geographical distribution patterns that were apparent by the end of the Early Permian. The Uralian, Franklinian, and Zechstein Seas contain a generally similar ectoproct fauna which is relatively low in diversity and associated with other faunas also having low diversity. Pakistan, India, and Australia also have lower ectoproct diversities at this time suggesting that in non-Tethyan regions, this was a time of increased extinctions, possibly because of ecological stress. The Tethyan ectoproct faunas continue to be highly diverse and apparently evolved nearly independently of other regions. A few of these Tethyan forms were able to disperse into other regions, as in the south-western United States, during this time, but a Tethyan faunal assemblage is clearly recognizable in contrast to one or more non-Tethyan assemblages.

The ectoproct distribution in the latest part of the Permian presents a number of difficulties for interpretation. For the most part, these ectoprocts are poorly known on a world-wide basis and this fact may be significant in itself. A number of genera persist in the Tethyan region, nearly all of which are continuations of earlier Tethyan endemic genera, and a few of these even extend into earliest Triassic strata. However, most of the Permian lineages became extinct either before, or early in, the latest Permian (Dzhulfian) and no completely acceptable explanation for this part of their evolutionary history has been made. In nearly all non-Tethyan regions latest Permian faunas in general are scarce and poorly known and this suggests abnormal marine environmental conditions were operating world-wide to reduce the faunas. Although mutual dependence on complex and obligatory community structure may be a possible factor, it seems more likely that rates of change in environmental conditions exceeded the abilities of the organisms to adapt.

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THE SPIRAL BRYOZOAN *TERE BELLARIA* FROM THE JURASSIC OF SOUTHERN ENGLAND AND NORMANDY

by P. D. TAYLOR

ABSTRACT. Morphological study of the monospecific genus *Terebellaria* has determined its unusual pattern of colony growth. Erect, almost cylindrical branches possessed an apical growth tip from which endozonal zooids were budded to extend the branch distally. A helico-spiral growth margin or, less commonly, a succession of annular growth margins, arose from the growth tip and progressed towards the colony base by budding exozonal zooids which were directed proximally so that their distal ends were nearer to the colony base than were their proximal ends. Multilamellar overgrowth of earlier-formed parts of the zoarium was thus achieved. Ontogenetic zones of feeding zooids, with open zooecial apertures and peristomes directed obliquely towards the colony base, occupied bands on the branch apex side of each whorl of the helico-spiral growth margin or each annular growth margin. The creation of a colonial water current system is suggested by this distribution of feeding zooids. Branch proliferation occurred by dichotomy at growth tips and also by 'adventitious' branch formation at exozonal growth margins proximal to the growth tip. By successively re-encrusting its erect branches, growth was relatively efficient, the zoarium was continually strengthened, and the establishment of an exogenous epifauna was hindered.

PERHAPS the most distinctive Jurassic bryozoan described is *Terebellaria ramosissima*, the only known species of the genus *Terebellaria*. Its screw-like colonies are particularly abundant in argillaceous basal beds of the English Forest Marble where they are a characteristic component of the well-known 'bradfordian' fauna (Palmer 1974). Because of its rather aberrant appearance, *T. ramosissima* has received attention in a number of works on bryozoans (Boardman and Cheetham 1973; McKinney 1975; Tavener-Smith and Williams 1972), but its three-dimensional morphology has never been fully described nor figured. *Terebellaria* is of further interest since it probably formed the basis on which Gregory (1896*a*) erected the cyclostome suborder Dactylethrata, which has since been rejected by Walter (1969), Hillmer (1971), and Brood (1972).

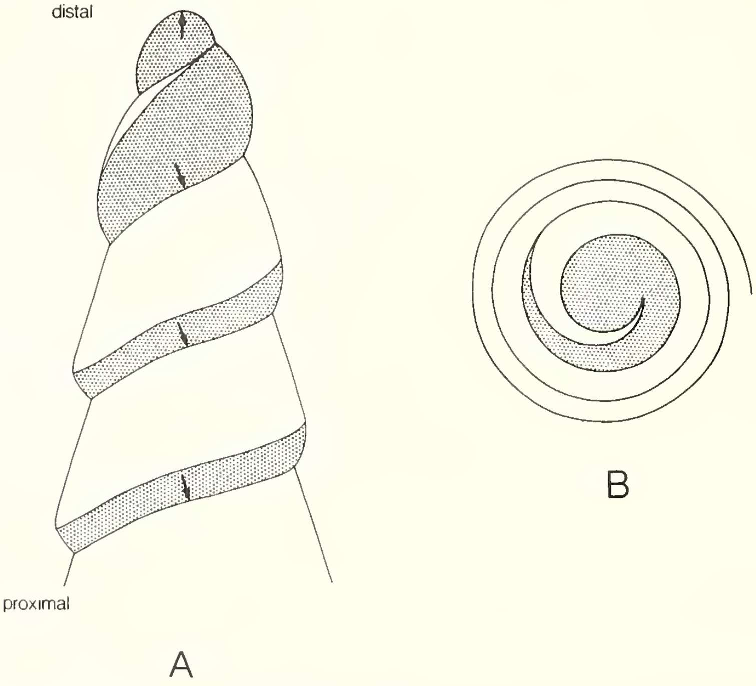
METHODS OF STUDY

External morphology was examined with the aid of a binocular microscope equipped with an eyepiece micrometer for quantitative determinations. Numerous thin sections and cellulose acetate peels were prepared by standard techniques (Boardman and Utgaard 1964; Nye, Dean, and Hinds 1972). Most of the sectioned specimens were initially embedded in an epoxy resin for ease of handling and to ensure that the outer surface of the specimen was preserved during peel preparation. Serial acetate peels at accurately predetermined intervals were obtained with the aid of a Croft grinder. Resin-mounted specimens for examination with the scanning electron microscope were cut and polished, etched with 0·1% formic acid for two minutes, and coated in a ten nannometre layer of gold.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 357–391, pls. 34–35.]

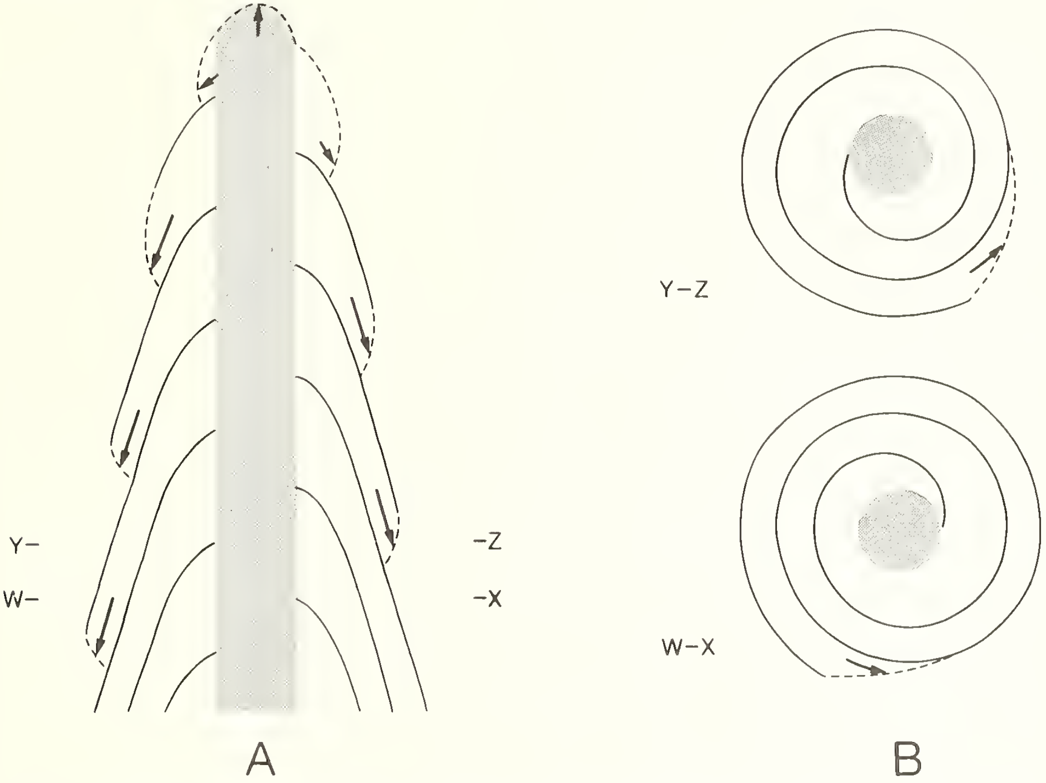
MORPHOLOGY

External. The erect zoarium of *T. ramosissima* (Pl. 34, figs. 1, 7) is usually screw-like in appearance (although some zoaria with a slightly different morphology will be considered later). Diagrams of an unbranched stylized zoarium (text-fig. 1), in which the extreme proximal parts are not shown, are used to illustrate the following morphological description. The proximally broadening screw-like form of the zoarium is defined by the growth margin (see Illies 1968, fig. 11; Taylor 1976, text-fig. 1) of open, partly formed zooecia which forms a series of whorls intervening with a ledge of zooecia complete with frontal walls. Zooecia exposed at the growth margin are directed towards the zoarial base and therefore, contrary to the situation found in most bryozoan colonies, their distal parts are nearer to the zoarial base than are their proximal parts. Zooecia situated between whorls of the growth margin form a shelf which slopes away from the zoarial axis towards the zoarial base. A thin lamina extends from the growth margin towards the zoarial base and covers some of the zooecia forming the shelf. The apex of the zoarium is formed by a growth tip laterally continuous with the screw-shaped or helico-spiral growth margin and similarly composed of open partly formed zooecia. However, open zooecia exposed at the



TEXT-FIG. 1. Simplified external aspects of a helico-spiral branch of *Terebellaria* from which the basal parts have been omitted. Stipple, growth margin and distal growth tip; arrows, directions of colony growth inferred from zooecial orientation. A, lateral aspect. B, colony viewed from above looking down on the growth tip; proximal whorls of the growth margin nearer the branch base are obscured by projecting ledges of zooecia.

growth tip are directed away from the zoarial base so that their distal extremities are also distal with respect to the zoarium as a whole. Both dextral (right-handed) and sinistral (left-handed) branches may occur. The distinction between them is particularly obvious on viewing zoaria from above when the growth margin may be seen to diverge from the growth tip in either a clockwise (dextral) or anti-clockwise (sinistral) manner.



TEXT-FIG. 2. Zoarial sections taken from the helico-spiral branch shown in text-fig. 1. Arrows indicate inferred growth directions at the growth margin and growth tip which are represented by broken lines. Solid lines mark zooecial frontal walls. A, longitudinal zoarial section; the axial region devoid of zooecial frontal walls is the endozone (grey). B, transverse zoarial sections taken at the two levels indicated on the longitudinal section; the origin of the spiral formed by zooecial frontal walls occurs on the periphery of the axial endozone (grey).

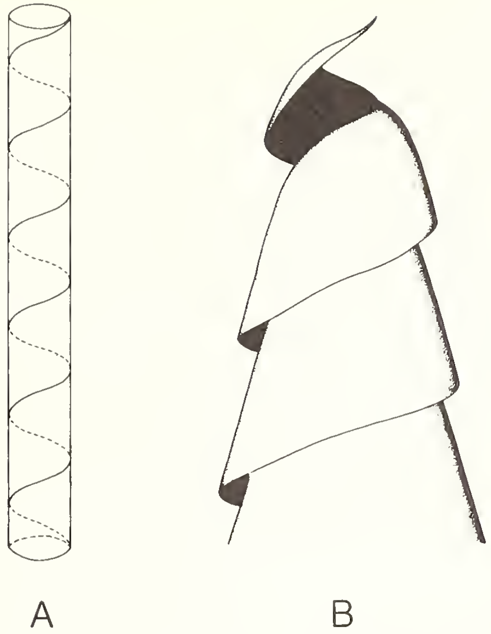
Internal. Internal structure has been revealed by preparing longitudinal and transverse zoarial sections.

Longitudinal sections show an axial endozone surrounded by a multilamellar exozone (text-fig. 2A). The endozone contains no zooecial frontal walls, lacks a budding lamina, and is exposed externally only at the apical growth tip. Zooecia arising in the endozone do so at divisions of interzooecial walls and are typically obliquely directed distally so that their distal extremities, formed by frontal walls, occur within the exozone. The exozone is laterally continuous with the endozone and, in longitudinal section, its layers appear to arise alternately from either side of the endozone (text-fig. 2A). Hence, endozonally budded zooecia form a series of stacked layers, well-defined distally but indistinct towards the core of the endozone. Endozonal zooecia within each layer are arranged so that the nearer the zoarial base they arise, the closer to the zoarial apex they terminate (text-fig. 7). Those arising nearer the base diverge at a small angle to the zoarial axis, but more distally arising zooecia may be reflexed by up to about 90° until they become perpendicular to the zoarial axis (Pl. 35, fig. 2). The most proximally arising, and thus most distally terminating, zooecia of each endozonal layer are for convenience here termed the 'omega' zooecia, although this does not imply that they are necessarily heterozooecia. More distally arising exozonal layers, bounded by a budding lamina and zooecial frontal walls, partly cover those which arise nearer the zoarial base. Successive exozonal layers terminate at consecutive whorls of the helico-spiral growth margin, as may be seen in longitudinal sections. Exozonal zooecia differ from those of the endozone because they arise at the junction between budding lamina and an interzooecial wall. Although longitudinal zoarial sections cut both endo- and exozonal zooecia longitudinally, those zooecia arising in the core of the endozone, including the omega zooecia, are somewhat obliquely sectioned because they are slightly twisted in the direction of spiral coiling of the zoarium.

Transverse zoarial sections (text-fig. 2B) show that the endozone, which appears to be a series of discrete layers when seen in longitudinal section, forms a continuous spiral in which later whorls overlap earlier ones. The budding lamina on which exozonal zooecia arise covers frontal walls of earlier zooecia in previous whorls (Pl. 35, fig. 5). The lamina describes an almost equable spiral (Thompson 1961, pp. 175–176) and has an eccentric origin on the surface of the axial endozone. Viewed from above, lamina spirals visible in transverse section (Pl. 35, fig. 1) may be either sinistral or dextral. However, the direction of spiral coiling will be opposite to that of the helico-spiral shape seen externally (cf. text-figs. 1B and 2B). Successive serial transverse zoarial sections show that the point of origin of the budding lamina rotates around the perimeter of the endozone. If the spiral seen in transverse section is sinistral, then its point of origin rotates in an anticlockwise direction between successively more distal sections towards the zoarial apex. If the spiral is dextral, then its point of origin rotates in a clockwise direction distally towards the zoarial apex. Most of the exozonal zooecia and centrally situated endozonal zooecia are cut transversely by zoarial transverse sections. However, the more reflexed endozonal zooecia, with long axes perpendicular to the zoarial axis, and some contiguous zooecia, are cut longitudinally by transverse zoarial sections (text-fig. 6A). The same zooecia are twisted slightly in the direction of the spiral described by the budding lamina. Thus, transverse zoarial sections reveal a distinctly asymmetrical arrangement of zooecia (Pl. 35, fig. 1). In a given transverse section, narrow proximal portions of astogenetically younger endozonal zooecia occur mainly on the axial side of the large omega zooecia in the vicinity of the exozonal origin point (text-fig. 6A). The narrow proximal portions of exozonal zooecia are observed where interzooecial walls bifurcate at their junction with the budding lamina.

Three-dimensional synthesis. The endozone forms an axial cylinder within which neither zooecial frontal walls nor a budding lamina occur. The axis of the endozonal cylinder is probably slightly helically twisted so that it attains an appearance

TEXT-FIG. 3. Three-dimensional aspects of the helico-spiral branch shown in text-figs. 1 and 2. A, the helical exozonal trace which represents the line along which axial walls of omega endozonal zooecia met the periphery of the endozone and gave rise to the exozonal budding lamina; shown solid when on the near side and dashed when on the reverse side of the cylindrical endozone. B, surface formed of zooecial frontal walls over which the exozonal budding lamina subsequently extends; its inner edge is the helical exozonal trace, its outer edge occurs at the growth margin which extends towards the colony base during growth.



approaching that of the complete *Zonopora* zoarium (Nye 1976, pl. 147). In *T. ramosissima*, the endozone is visible externally only at the hemispherical growth tip where new endozonal zooecia arise and diverge such that their distal parts occur within the exozone. Exozonal zooecia arise at the margin of a basal budding lamina, which extends as a helico-spiral coil towards the zoarial base partly covering previously formed zooecia. The point at which the exozone emerges from the surface of the cylindrical endozone is defined by the appearance of the budding lamina. The axial edge of this lamina describes a helical trace, here termed the exozonal trace, on the surface of the endozone (text-fig. 3A). Both sinistral and dextral exozonal trace helices are known in *T. ramosissima* and the direction of helical coiling determines directly whether the helico-spiral seen externally is sinistral or dextral. The form of the laminate surface composed of zooecial frontal walls (text-fig. 3B) reveals the involved three-dimensional morphology of the exozone.

SPIRAL GROWTH

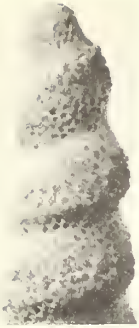
Growth in bryozoan colonies is achieved largely by zooidal addition. Borg (1926) showed that zooidal budding in extant cyclostomatous bryozoans occurs in regions of the colony enclosed beneath a common or hypostegal coelom which he termed the 'common bud'. Here, interior body walls are secreted by epithelial tissue which lines them on both sides (Boardman and Cheetham 1973). New zooids are partitioned off by division of these interzooidal walls. Elsewhere hypostegal coelom is lacking and zooidal budding does not usually occur (cf. peristomal budding described by Harmelin 1974). Zooidal growth away from the common bud is limited to the lengthening of exterior body wall, such as peristomes and zooecial frontal walls, secreted from one side only. In fossil tubuloporinidean cyclostomes partly formed zooecia with incomplete frontal walls (exterior body wall) and having their interzooecial walls (interior body wall) exposed are characteristic of regions in which zooidal budding was occurring during life. By analogy with extant taxa, these regions were covered by hypostegal coelom. The helico-spiral growth margin and apical growth tip clearly constituted the common bud of *T. ramosissima* colonies and were enclosed beneath a continuous hypostegal coelom within which new zooids became partitioned off by the division of expanding interior body walls. Zooidal budding caused the growth margin and growth tip to advance and leave behind zooids, no longer in coelomic continuity with one another, which are represented by those zooecia occupying the ledge between whorls of the helico-spiral growth margin.

The morphology of *T. ramosissima* contrasts with that of most other erect tubuloporinidean cyclostomes which have an apical growth tip from which zooecia are budded to lie in a distally divergent orientation. This morphology characterizes so-called vinculariiform zoaria such as *Pustulopora* (Brood 1972, p. 95) where zooidal budding does not occur proximal of the growth tip. Transverse zoarial sections are almost identical to those aspects of the zoarium seen by looking down on the growth tip. Successively more distal transverse sections approximate to discrete growth stages for no further zooecia can be added in the plane of section. However, the helico-spiral growth margin of *Terebellaria* is intersected by all transverse zoarial sections and transverse sections do not thus correspond to distinct growth stages for further zooecia may be added in the plane of section. In addition, external aspects of the zoarium seen by looking down on the growth tip do not approximate in appearance to transverse zoarial sections (cf. text-figs. 1B and 2B).

Zooecial budding. Two distinct modes of zooecial budding occurred in *Terebellaria* colonies. At the apical growth tips of the colony endozonal zooecia were budded by division of interzooecial walls at triple junctions between established zooecia. Newly budded zooecia occupy space partitioned off from more than one established zooecium, a budding style termed interzooecial by McKinney (1975). Endozonal zooecial budding had a locus on the axial walls of omega zooecia (text-fig. 8).

EXPLANATION OF PLATE 34

Figs. 1–9. *Terebellaria ramosissima* Lamouroux. Bathonian. 1, BMNH 11510c, distal portion of a dextral branch showing the apical growth tip and helico-spiral growth margin, ?locality, × 7. 2, BMNH D4518, parts of three growth margins proximal to a branch dichotomy showing ontogenetic zonation of zooecia, Ranville, × 8. 3, BMNH 60215, portion of a zoarium in which all zooecia and the growth margin (centre) are occluded, Ranville, × 10. 4, BMNH 11510d, the opposite end of the horizontal growth margin division shown in text-fig. 9. A zoarial lateral wall extends across the dislocation (arrowed), ?locality, × 7. 5, BMNH 60215d, zoarial fragment with a branch dichotomy, Ranville, × 2·3. 6, BMNH 60360b, adventitious branch (right) arising from a parent branch with occluded growth margins, Ranville, × 7. 7, BMNH D1812q, incipient dichotomy at the tip of a dextral branch, Bradford-on-Avon, × 7. 8, BMNH D52637, ovicell with ooeciopore (arrowed), St. Aubin-sur-mer, × 15. 9, BMNH 60360a, zoarium showing a common preservation in which the zooecial frontal walls have been removed by abrasion, Ranville, × 6.



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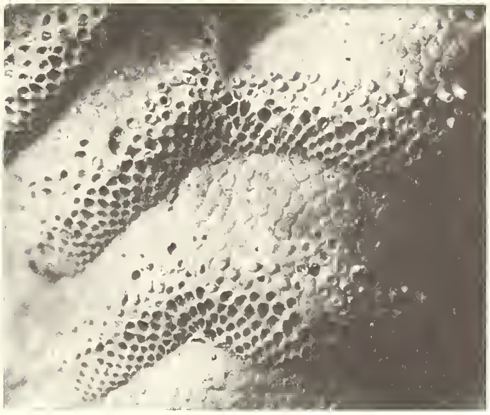

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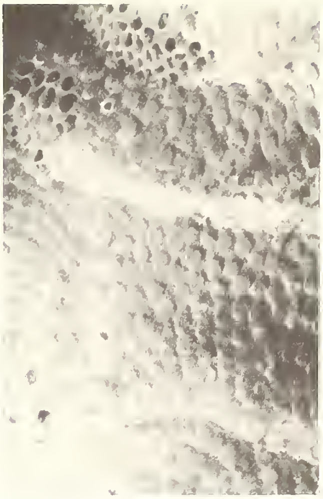

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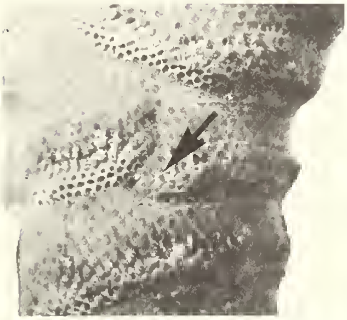

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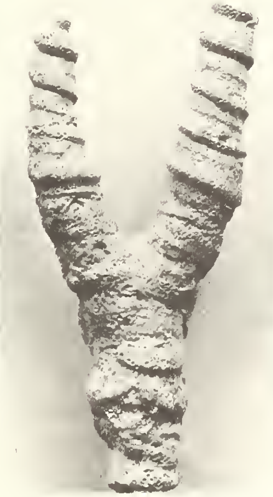

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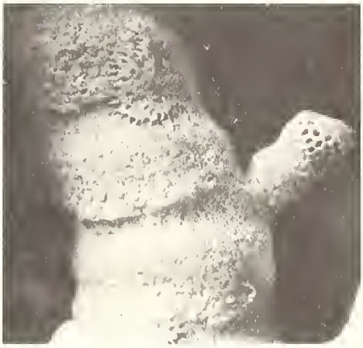

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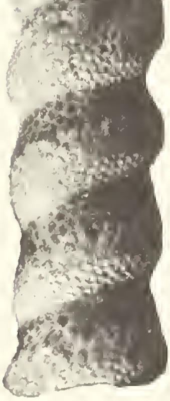

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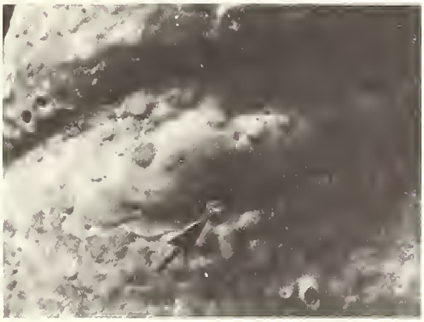

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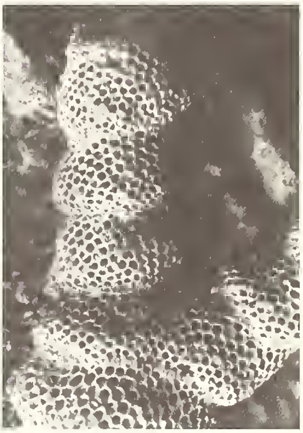

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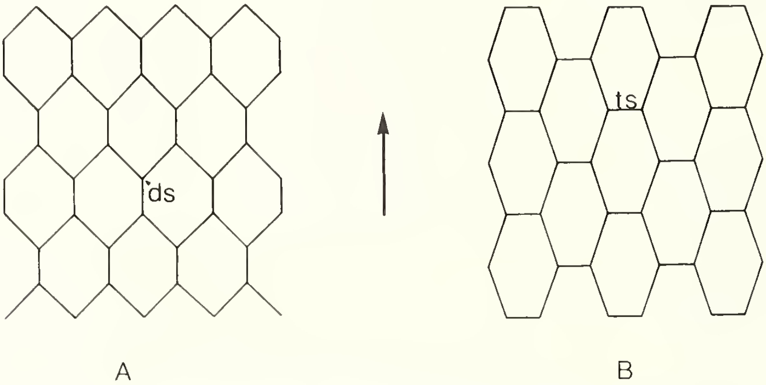
TAYLOR, *Terebellaria ramosissima*

Exozonal budding at the helico-spiral growth margin occurred within a basal prolongation of the same hypostegal coelom as that which covered the growth tip. However, exozonal zooecia were budded at junctions between interzooecial walls and the budding lamina. The budding lamina was apparently an exterior body wall of the type which invariably exists at the attached bases of cyclostome colonies. The pattern of zooecial budding on this lamina compares with that known in many other cyclostome taxa (Borg 1926; Boardman and Cheetham 1973; Illies 1968). An almost perpendicular rudimentary interzooecial wall, or septum, divides where it meets the budding lamina producing a triangular cavity forming the proximal part of a zooecium. During further growth the cavity enlarges until its sloping interzooecial lateral walls coalesce with identical walls belonging to adjacent zooecia. Such coalescence causes the formation of a vertical interzooecial wall of a new generation. This type of budding pattern produces a characteristic pattern of septal traces which delineate the basal parts of elongate hexagonal zooecia developing on the budding lamina (text-fig. 4A). The long axis of each zooecium bisects the angle formed between pairs of oblique distal and proximal walls. The septal trace pattern is frequently repeated where the interzooecial walls meet the frontal surface of the zoarium. An alternative type of septal trace pattern (text-fig. 4B) predominates in *T. ramosissima.* It results from new zooecia being partitioned off by the formation on the budding lamina of a transverse septum linking two previously formed vertical septa. The transverse septum slopes upwards to meet the zoarial surface distally. Long axes of zooecia bisect



TEXT-FIG. 4. Septal trace patterns formed where interzooecial walls meet a basal budding lamina. The pattern is usually repeated distally where the interzooecial walls contact the zoarial surface formed of zooecial frontal walls. Growth direction is indicated by an arrow. A, normal tubuloporinidean septal trace pattern. New zooecia are partitioned off by division of an established interzooecial wall or septum (ds). In plan, zooecia are hexagonal with their long axes bisecting, both proximally and distally, the angle made between pairs of oblique interzooecial walls. B, alternative septal trace pattern common in *Terebellaria.* The formation of an inclined transverse septum (ts) partitions off a new zooecium. As a result, zooecia are hexagonal with their long axes bisecting, both proximally and distally, interzooecial walls or septa which lie transverse to growth direction.

transverse septa at both ends of elongate hexagonal zooecial bases. Borg (1926, fig. 39, septum 'y') noticed that zooecial budding of this type occurred occasionally in normal tubuloporinidean budding patterns where it produced zooecial proliferation by intercalating an additional zooecium.

Endozonal and exozonal zooecia are not considered to be polymorphically distinct from one another despite their different budding modes. There is continuous variation in quantitative morphological characters between the most axial endozonal zooecia (omega zooecia) and exozonal zooecia. By analogy with extant cyclostomes, exozonal zooecia are certainly autozooecia and occasional preservation of conventional peristomes in endozonal zooecia suggests that they too are autozooecia.

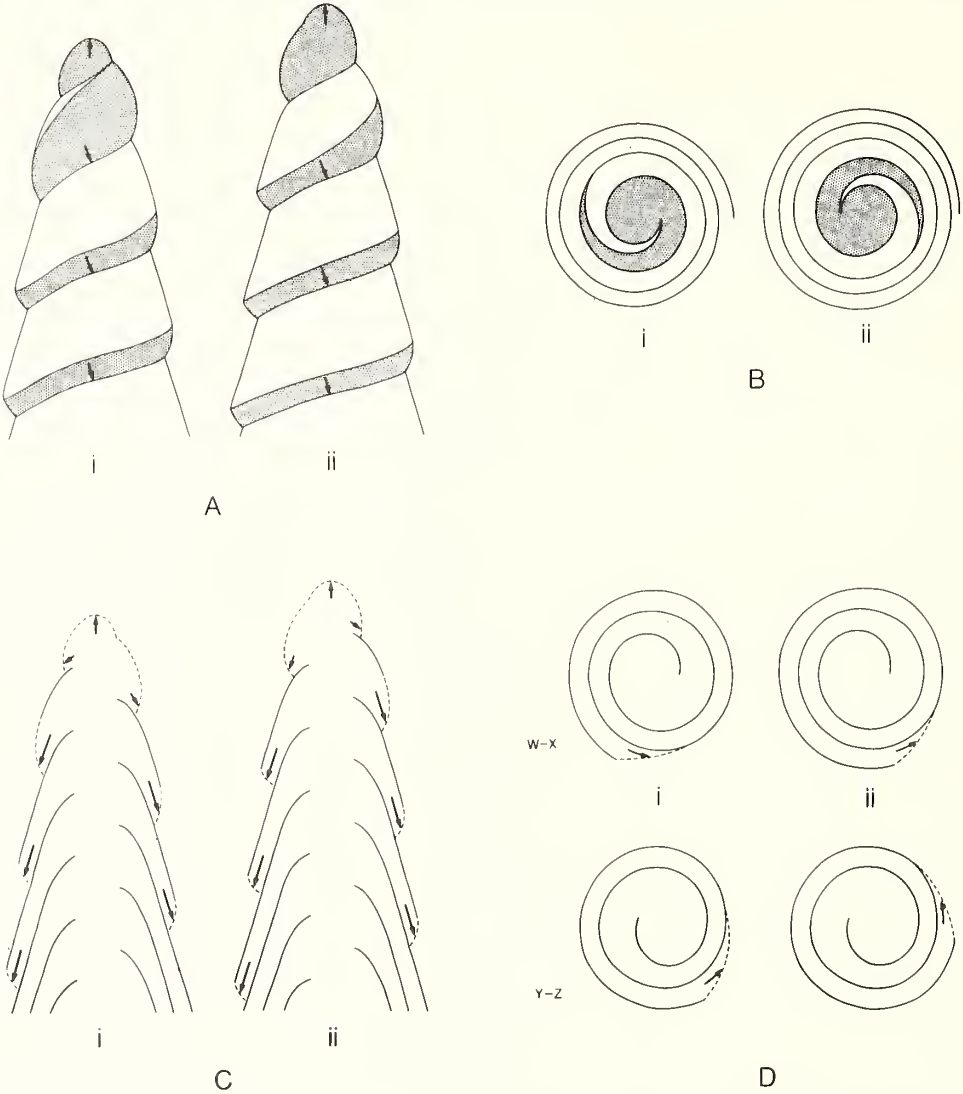
Growth pattern. To determine patterns of growth in fossil cyclostomes it is necessary to recognize the regions in which zooids were being budded immediately prior to colony death, and to infer previous positions and attitudes of zooidal budding regions. As growth in all bryozoans occurs in a proximal to distal direction, the direction of local colony growth may be determined by recognizing the proximal and distal parts of zooecia. *T. ramosissima* zooecia are narrow proximally but become broader distally and develop a frontal wall with a distal aperture where they rise obliquely to meet the zoarial surface. Exozonal zooecia are usually orientated with their long axes almost parallel to the zoarial long axis, and with their distal ends closer to the zoarial base, indicating that they grew towards the colony base. Conversely, endozonal zooecia typically have their distal ends nearer to the zoarial apex, indicating growth away from the colony base. The attitudes of preserved budding regions confirm these conclusions for exozonal growth margins face the zoarial base, but the endozonal growth tip is directed away from the zoarial base (text-fig. 1A). Therefore, exozonal growth towards the colony base accompanied endozonal growth, extending the colony distally.

Long axes of endozonal zooecia meet the surface of the almost hemispherical growth tip at right angles. Zooecia are asymmetrically distributed over the growth tip with respect to their size. Smaller, more recently budded, zooecia are concentrated slightly axially of large omega endozonal zooecia of the preceding helical whorl. Hence, the locus of endozonal budding is eccentrically situated relative to the central axis of the zoarium. Distal colony extension apparently caused rotation of the locus of endozonal budding in unison with the point of exozonal origin.

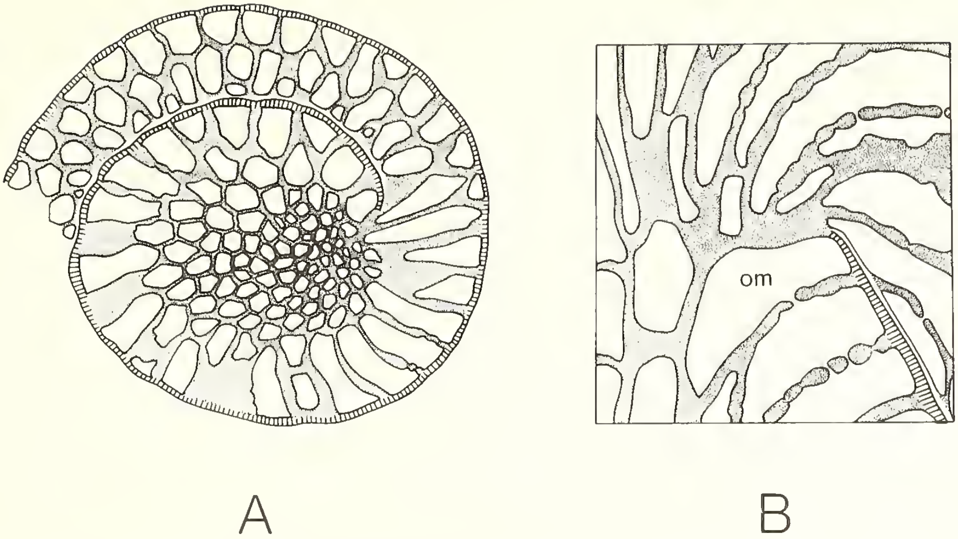
The essentially linear helicospiral growth margin compares with growth margins known from many adnate tubuliporinidean taxa. Long axes of newly budded zooecia are perpendicular to the length of the growth margin and thus make a small angle with the long axis of the *T. ramosissima* zoarium. A helico-spiral growth margin was typically maintained throughout growth, but its whorls progressed towards the colony base whilst the helico-spiral was lengthened as endozonal growth extended the colony distally.

To illustrate the inferred mode of colony growth, an arbitrary increment of growth (text-fig. 5) has been added to the stylized zoarium originally shown in text-figs. 1 and 2. Exterior lateral aspects (text-fig. 5A) show the simultaneous effect of distal colony extension and basalward exozonal growth, which lengthen and broaden the zoarium respectively. The position of divergence from the growth tip of the helico-spiral growth margin, and the locus of endozonal budding, both rotate by 180° in a clockwise direction when the growth increment is added (text-fig. 5B). Translation produced by distal colony extension combined with this rotatory motion cause the exozonal trace to be helical in form (text-fig. 3A). Comparison of transverse sections cut at equivalent positions on the zoarium before and after addition of the growth increment (text-fig. 5D) show clockwise extension of the overgrowing spiral exozone.

Variations in over-all proportions observed between natural zoaria can be related to variations in the relative growth rates of endozone and exozone, or to the rate of



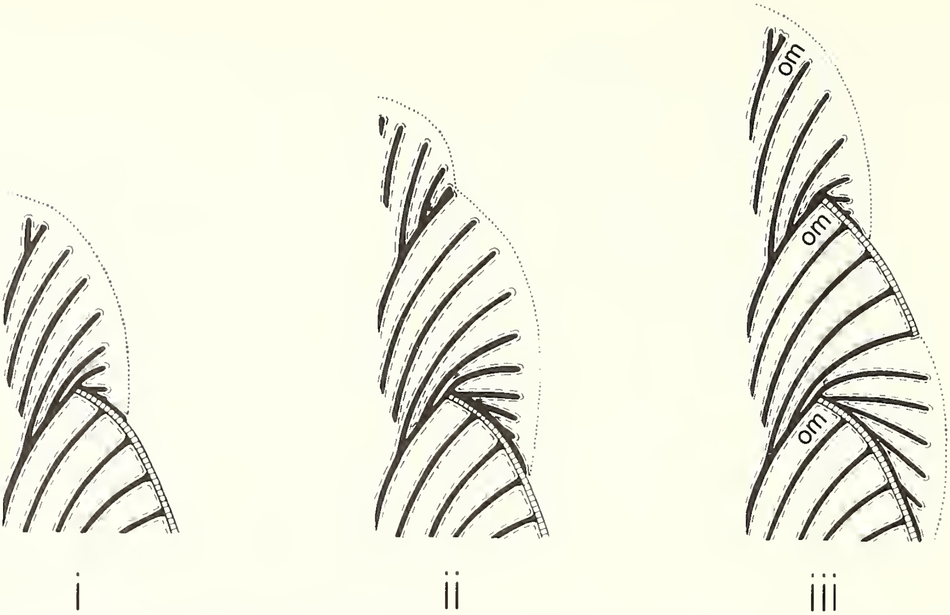
TEXT-FIG. 5. Addition of an arbitrary increment of growth to the helico-spiral branch illustrated in text-figs. 1–3. In all cases diagrams labelled 'i' are before growth, 'ii' after growth. A, external lateral aspects. B, external aspects viewed from above the distal growth tip. C, longitudinal zoarial sections. D, transverse zoarial sections.



TEXT-FIG. 6. Camera lucida drawings to illustrate zooecial configuration in sections of helico-spiral branches of *Terebellaria ramosissima.* Stipple, interzooecial walls; white, basal budding lamina; hatched, zooecial frontal walls. A, part of transverse zoarial section showing an axial endozone, lacking zooecial frontal walls, in which zooecia are sectioned approximately transversely. The endozonal budding locus is the region occupied by the smallest zooecia. Strongly reflexed zooecia near to the boundary between endozone and exozone are almost longitudinally sectioned; BMNH D2111g, 'Bathonian, Ranville'. × 19. B, part of a longitudinal section at the transition between endozone and exozone. The axial interzooecial wall of an omega endozonal zooecium (om), slightly obliquely sectioned, gives rise to its own frontal wall (stippled) and the exozonal budding lamina which covers it. Endozonal budding has a locus above the axial wall of the omega zooecium. Interzooecial walls have pores and constrictions; BMNH D2111j, 'Bathonian, Ranville'. × 39.

rotation of the exozonal origin point. If the endozone grew more rapidly than the exozone a slender zoarium resulted, whilst the converse situation would have produced a zoarium broadening rapidly towards its base. A relatively rapid rotation of the exozonal origin point would have produced a tight exozonal helical trace and a zoarium in which the distance between successive whorls of the helico-spiral growth margin is small.

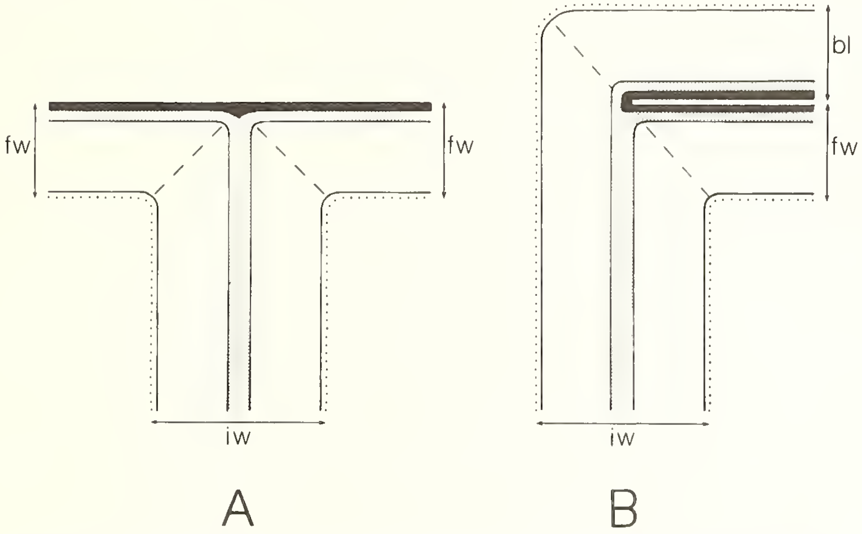
Transition zone interpretation. The zone of transition between endozone and exozone (Pl. 35, fig. 4) deserves further attention, for here the mode of zooecial budding altered and a partial splitting or 'unzipping' of the colonial common bud may be inferred. The nature of the transition is explained by reference to text-fig. 7, which shows a growth series of longitudinal half sections on which are marked probable positions of epithelia during life. At growth stage 'i' extension of endozonal zooecia was occurring by distal growth of interzooecial walls beneath the hypostegal coelom of the growth tip. Zooecia which later contributed to the endozone of the succeeding helical whorl were budded off predominantly from the axial wall of the omega zooecium in the plane of section (text-fig. 6B). When interzooecial walls of the omega zooecium contacted the



TEXT-FIG. 7. Interpretation of growth at the transition between endozone and exozone in *Terebellaria*. Longitudinal half sections of three growth stages, 'i'–'iii'. For detailed explanation of the sequence of events see text. Interzooecial walls and budding lamina, black; zooecial frontal walls, hatched; inner epithelium lining interzooecial walls, dashed line; outer epithelium, dotted line; omega zooecia, om. The hypostegal coelom of the common bud (growth tip and growth margin) is enclosed between the inner and outer epithelia. Zooecial apertures have been omitted for simplicity.

outer epithelium (growth stage 'ii') the zooecium lost hypostegal coelomic connection and growth of its frontal wall began. This contact with the outer epithelium delineates the outer surface of the cylindrical endozone. Further endozonal zooecia of the same helical whorl, but progressively nearer the colony base, also contacted the terminal membrane and began to form frontal walls. In this way, within the plane of section, the hypostegal coelom of the growth tip had become separated from that of the basally extending growth margin by an intervening area of zooecia which possess calcified exterior body walls. Laterally contiguous exozonal zooecia then also began to form calcified exterior body walls (growth stage 'iii'). Endozonal zooecia of the succeeding helical whorl had continued to extend upward by lengthening their interzooecial walls beneath the hypostegal coelom of the growth tip. At the same time, exozonal zooecia were formed on a budding lamina which began to overgrow the frontal wall of the omega zooecium from the preceding helical whorl. The budding lamina thus appears to develop immediately above the position at which the frontal wall of the omega zooecium from the preceding helical whorl met the endozone. The lamina is of course laterally continuous off the plane of section, with the lamina flooring exozonal zooecia budded in previous whorls of the helix. As the lamina extended towards the colony base zooecia of the exozone were budded on it.

The helical exozonal trace (text-fig. 3A) is the line along which diverging axial interzooecial walls of omega zooecia meet the surface of the cylindrical endozone. At this contact each interzooecial wall bifurcates to form the frontal wall of the omega zooecium and the exozonal budding lamina which subsequently overgrows that frontal wall. The exozonal budding lamina is apparently a type of exterior body wall homologous with the basal laminae, upon which cyclostome colonies are commonly founded. Hence, when the axial interzooecial wall, an interior body wall, of the omega zooecium contacts the surface of the endozone it divides to form two exterior body walls of different type, a zooecial frontal wall and a budding lamina. An analogy may be made between this division and that commonly observed in which an interzooecial wall divides to give two zooecial frontal walls (text-fig. 8A). If one of the frontal walls is rotated by 180° until it lies directly upon the other (text-fig. 8B) then the situation occurring at axial omega zooecial wall division in *T. ramosissima* is achieved. The rotated frontal wall apparently must now become an exterior body wall of the basal lamina type for its cuticle is juxtaposed with a substratum, the frontal wall of the adjacent zooecium. The omega zooecium began to be overgrown by the budding lamina soon after its frontal wall had formed, but frontal wall formation in zooecia nearer the colony base progressed more rapidly than extension of the budding lamina and a separation of about 2 mm was achieved.

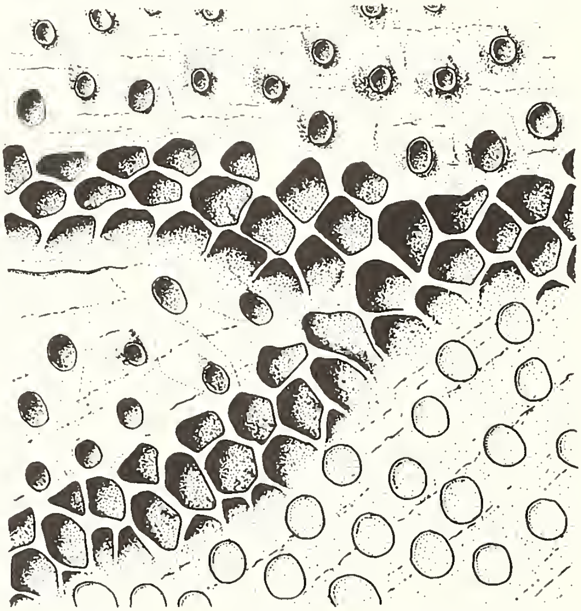


TEXT-FIG. 8. Dichotomies of interzooidal walls (interior body wall) to form two exterior body walls. A, normal type of dichotomy (after Brood 1972, fig. 7D; Hinds 1975, text-fig. 1). The interzooidal wall (iw) is composed of a primary skeletal layer (stippled) flanked by secondary skeletal layers (white) bordered by secretory epithelia (dotted line). It divides to form two zooecial frontal walls (fw) composed of a surficial cuticle (black) underlain by a primary skeletal layer, which overlies a secondary skeletal layer and secretory epithelia. Arbitrary boundary between the interzooidal wall and the frontal walls is a dashed line. B, dichotomy inferred to have occurred in the omega zooecia of *Terebellaria* when their interzooidal walls met the periphery of the endozone. The interzooidal wall (iw) divides to form a zooecial frontal wall (fw) and a basal budding lamina (bl) which subsequently covers the frontal wall.

Occasionally the exozonal growth margin divided into two in a plane parallel to the budding lamina by the formation of a new budding lamina midway between the original lamina and the frontal surface of the zooecial layer. This type of division (text-fig. 9) probably also required bifurcation of an interzooecial wall to form a zooecial frontal wall and a new, overgrowing, budding lamina. The dichotomy contrasts with that of omega zooecial axial walls because the growth margin beneath grew more rapidly than that above the division. Such horizontal growth margin division began at a particular point and spread laterally along the growth margin in one direction only. Meanwhile, distal growth from the initial point of appearance of the split caused the formation of a zoarial lateral wall (Pl. 34, fig. 4) comparable to those produced by migrating pivot points in other cyclostomes (Taylor 1976, p. 302). Growth margin horizontal division apparently also occurs in the extant bereniciform species *Plagioecia platydiscus* described by Harmelin (1976).

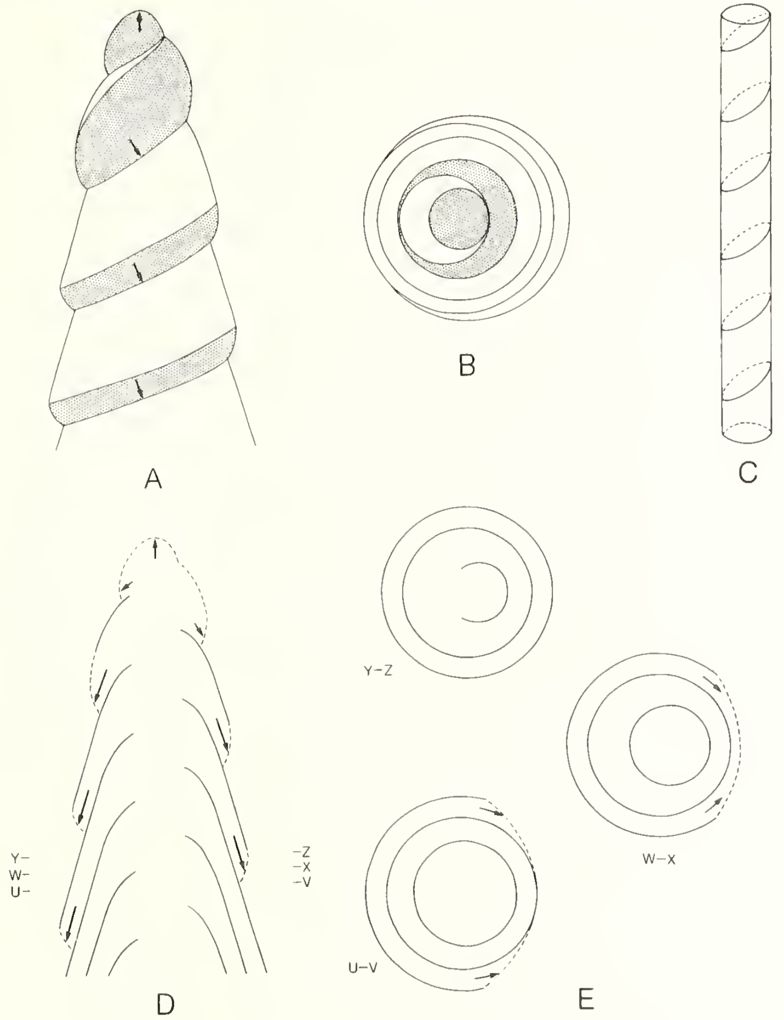
ANNULAR GROWTH

Although the exozonal growth margin in *T. ramosissima* is normally a helico-spiral, a second situation may occur in which the exozone is composed of a series of discrete ring-shaped or annular growth margins. Branch dichotomies frequently result in at least one of the daughter branches having exozonal growth margins of this type. Annular growth margins are about the same distance apart as the successive whorls of



TEXT-FIG. 9. Camera lucida drawing showing part of the exterior of a *Terebellaria ramosissima* zoarium in which horizontal division of the growth margin was occurring. A split in the growth margin was apparently extending from left to right; BMNH 11510d, 'Great Oolite ?locality'. × 34.

a helico-spiral growth margin, and they are usually inclined with respect to the zoarial axis. Transverse zoarial sections, instead of revealing a spiral exozone, show discrete exozonal layers, each floored by a budding lamina, arranged in an off-centred concentric pattern (text-fig. 10E). The number of concentric zooecial layers present in a transverse section indicates the number of growth margins which have overgrown that part of the colony. Longitudinal zoarial sections (text-fig. 10D) may be indistinguishable from similar sections taken from branches with helico-spiral growth margins.



TEXT-FIG. 10. *Terebellaria* branch with an annular exozone. Legend as in text-figs. 1–3. A, external lateral aspect. Compare with text-fig. 1A. B, external aspect looking down upon the distal growth tip. Compare with text-fig. 1B. C, inclined annular exozonal traces occurring on the periphery of the cylindrical endozone. Compare with text-fig. 3A. D, longitudinal zoarial section. Compare with text-fig. 2A. E, transverse zoarial sections taken at the levels marked on the longitudinal section. Compare with text-fig. 2B.

Colonies have the same cylindrical endozone as those possessing a helico-spiral growth margin, and have zooecia typically directed distally in the endozone and basally in the exozone. In three dimensions the exozonal layers take the form of a series of stacked cones truncated where they meet the endozone. Traces on the cylindrical endozone marking the point of origin of the exozone are thus a succession of inclined rings (text-fig. 10C). Some transverse zoarial sections reveal two points of origin for the innermost exozonal layer, whilst others have no points of exozonal origin. Sections of the former type are located at positions where the innermost off-centred budding lamina intersects the cylindrical endozone and is crescent-shaped. Those of the latter type occur at positions which have no such intersections and the innermost budding lamina is annular.

Stylized diagrams (text-fig. 10A, B) illustrate the external appearance of a branch with annular growth margins. Transverse zoarial sections have been cut serially in the direction of distal colony extension (text-fig. 10E). In section U–V the innermost budding lamina forms a complete ring for it has no intersection with the endozone. The diameters of all budding laminae decrease distally towards the branch apex, in accordance with their conical three-dimensional form, until in section W–X the innermost budding lamina almost intersects the left side of the endozone. Distal to W–X this innermost lamina is crescent-shaped and has two points of exozonal origin in the plane of section. Its diameter continues to decrease towards the colony apex, for example at section Y–Z. The budding lamina last occurs at the extreme right of the endozone before disappearing from the plane of section. The diameters of other exozonal rings also decrease distally, and the lamina which is now innermost occupies a position equivalent to that of the innermost lamina in section U–V.

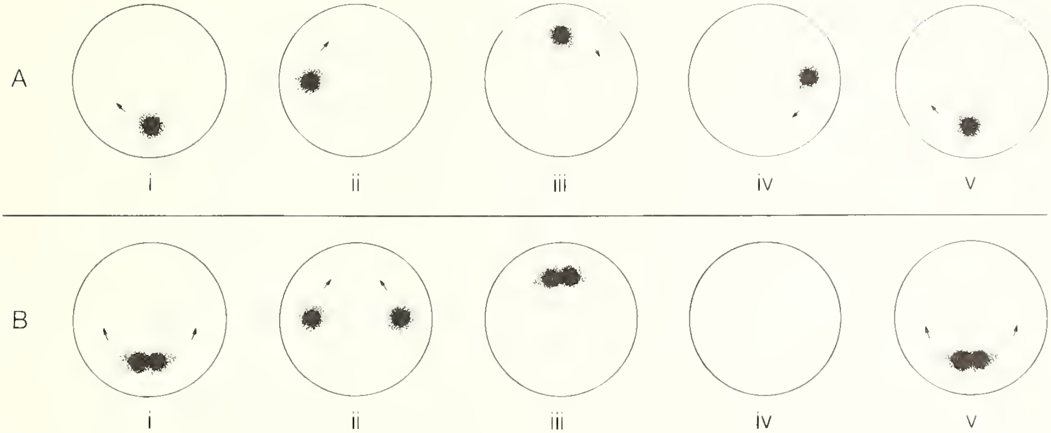
Longitudinal zoarial sections (text-fig. 10D) reveal an identical mode of derivation of the exozone from the endozone in both spiral and annular growth. In branches displaying an annular exozone the endozone can again be partly divided into layers. Each layer is produced by endozonal zooecial budding centred on axial walls of omega zooecia belonging to the preceding layer. However, exozone was produced continuously in branches with a helico-spiral growth margin, but discontinuously in those with annular growth margins where periods of new exozonal layer formation at the growth tip would have alternated with intervals of endozonal extension without formation of new exozonal layers. By inference, hypostegal coeloms enclosing individual growth margins became successively divided from the hypostegal coelom covering the growth tip.

The distinction between branches with a helico-spiral growth margin and those with annular growth margins may be explained in terms of movement of the endozonal budding locus. The type of movement apparently dictated the form of the exozonal trace which in turn determined zoarial external appearance. Rotation of the endozonal budding locus in one direction only, combined with the translatory motion of distal growth (text-fig. 11A), would produce a helical exozonal trace and a helico-spiral growth margin. Distal growth accompanied by division of the endozonal budding locus, followed by rotation of the two consequent loci in opposite directions and their eventual meeting at the other side of the endozone (text-fig. 11B) would produce a branch with annular exozonal traces and annular growth margins.

BRANCH PROLIFERATION

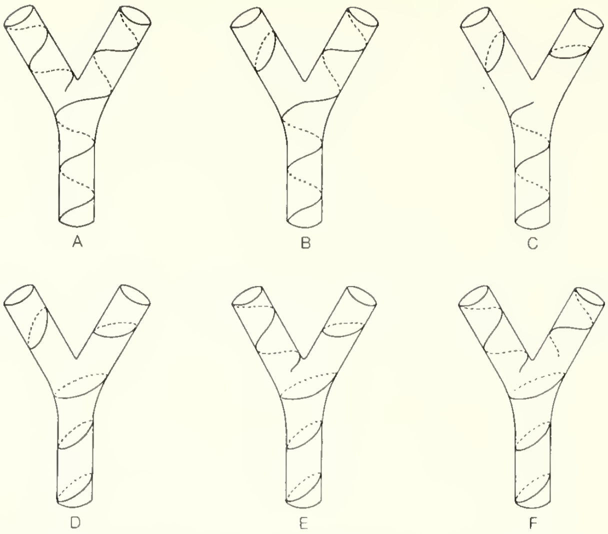
There are two distinct modes of branch proliferation in *T. ramosissima.* Primary branching occurred by dichotomy at apical growth tips, and secondary or adventitious branching by development of daughter branches at exozonal growth margins.

Primary branching. Equilateral division at the branch apex formed two daughter branches which diverged from one another at an angle between 30° and 70° (Pl. 34, fig. 5). Zoarial sections show that branch dichotomy involved a splitting of the cylindrical endozone. Immediately prior to division, the endozone became elliptical in cross-section by increasing its diameter within the plane in which the division was to occur. Subsequent constriction of the ellipse midway along its major axis culminated in eventual division of the endozone into two. This pattern of endozonal division is also characteristic of other cyclostomes possessing cylindrical branches with apical growth tips. In *T. ramosissima,* however, the presence of a layered exozone complicated the growth pattern produced by dichotomy.



TEXT-FIG. 11. Diagrammatic transverse zoarial sections showing rotation of the budding locus (stippled) within the circular endozone during distal branch extension in *Terebellaria.* Five growth stages, 'i'–'v'. A, clockwise rotation giving rise to a branch which is a dextral helico-spiral externally. B, division of the locus and rotation of the two consequent loci in opposite directions prior to their coalescence at the opposite side of the endozone. A new locus forms after an interval of time in which there is no endozonal budding locus. A branch with inclined annular growth margins is produced by this sequence of events.

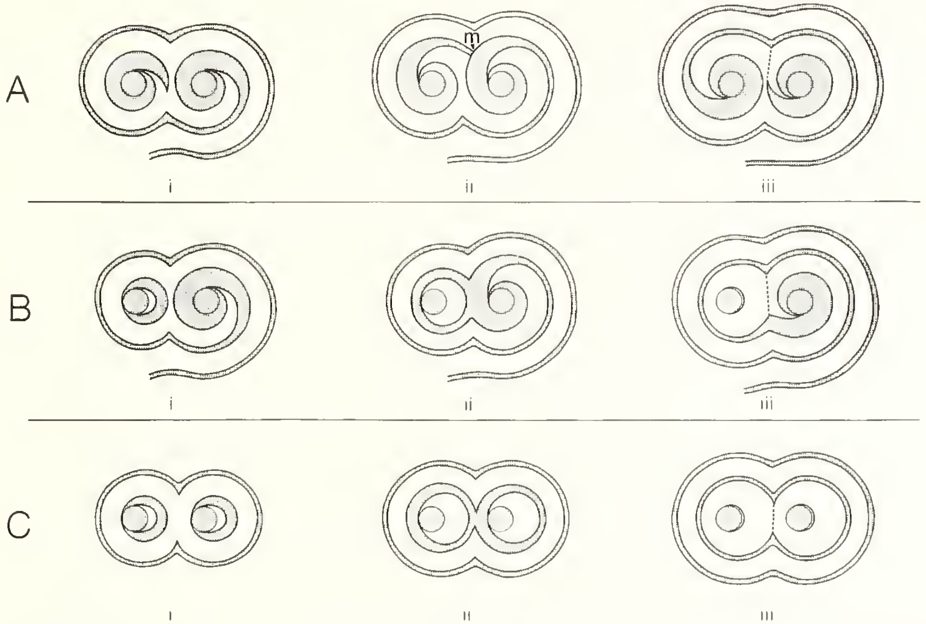
The effect on the exozone of endozonal dichotomy is most suitably examined by considering changes in the form of the exozonal trace. The parent branch may have either a helical or an annular exozonal trace reflecting spiral and annular modes of growth respectively. Both daughter branches may have helical or annular exozonal traces, or one may have a helical and the other an annular exozonal trace. Therefore,



TEXT-FIG. 12. The six possible modifications of the exozonal trace consequent upon primary branching. A, B, and E have been positively identified in fossil zoaria. A, parent branch and both daughter branches have helical traces. B, parent branch and one daughter branch have helical traces, the second daughter branch has annular exozonal traces. C, parent branch has a helical trace, both daughter branches have inclined annular traces. D, parent branch and both daughter branches have annular traces. E, parent branch and one daughter branch have annular traces, the second daughter branch has a helical trace. F, parent branch has an annular trace, both daughter branches have helical traces.

there exist six alternatives for exozonal trace pattern changes during dichotomy (text-fig. 12). Types A, B, and E of text-fig. 12 have been positively identified in fossil zoaria. In types A, E, and F new helical exozonal traces had to be initiated on one or both daughter branches after endozonal division. This was achieved by the formation of a new series of omega zooecia whose axial walls on reaching the outer epithelium gave rise to frontal walls and a budding lamina. The exozonal trace on the parent branch of types A and E apparently continues up one of the daughter branches. If one or both of the daughter branches display spiral growth it is always in the same spiral direction (sinistral or dextral) as that of their parent branch. In this respect, *Terebellaria* differs from two other well-known bryozoan genera which exhibit spiral growth forms. In both *Archimedes* (Condra and Elias 1944; Cowen and Rider 1972) and *Zonopora* (Nye 1976) spiral branches dichotomize to give daughter branches, one of which spirals in the same direction as the parent branch, and one in the opposite direction.

Further complications in growth pattern occurred when basally extending exozonal growth margins of daughter branches met one another at their confluence with the parent branch. Discrete growth margins belonging to the same *Terebellaria* colony had the ability to coalesce or anastomose on meeting (Pl. 34, fig. 2) and to grow in unison thereafter. Anastomosis of this type is known to occur in some extant bryozoans and other colonial organisms, and has been termed autosyndrome (Knight-Jones and Moyse 1961; Stebbing 1973; Ryland 1976, pp. 401–409). In *T. ramosissima* the effects of growth margin convergence and anastomosis are difficult to illustrate, as their comprehension ideally requires the use of three dimensions. Diagrammatic external aspects showing three growth stages of three dichotomies are given to illustrate the convergence of two helico-spiral growth margins (text-fig. 13A), a helico-spiral and an annular growth margin (text-fig. 13B), and two annular growth margins (text-fig. 13C).

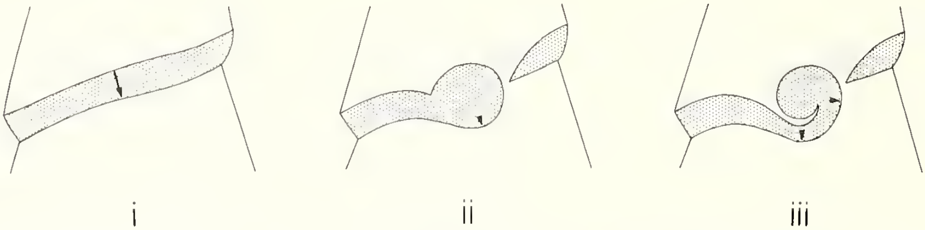


TEXT-FIG. 13. The effect of convergence between basally extending exozonal growth margins of daughter branches at their junction with the parent branch. Diagrammatic external aspects looking down on the distal growth tips. For simplicity and clarity, the effects of angular divergence of daughter branches, and of overlap of more proximal parts of growth margin by autozooecial ledges (as in text-fig. 1B) have been ignored. Three growth stages ('i'–'iii') are illustrated for each of three examples (A–C). Growth margins and growth tips, stippled; lines of anastomosis, dashed. Circular axial parts of the growth tips are endozones.

A, convergence of helico-spiral exozonal growth margins. At growth stage 'i', the helico-spiral margin of the right-hand daughter branch is continuous with that of the parent branch, but that of the left-hand daughter branch terminates at its confluence with an autozooecial ledge on the right-hand daughter branch. Further growth ('ii') results in the meeting (m) of helico-spiral growth margins belonging to each daughter branch. Anastomosis between them occurs and causes the development of a discontinuity in the left-hand helico-spiral growth margin. The helico-spiral growth margin of the parent branch now ('iii') appears to be continuous with that of the left-hand daughter branch, whilst that of the right-hand daughter branch abuts against a ledge of autozooecia on the left-hand branch. B, convergence of a helico-spiral growth margin with an annular growth margin. Anastomosis of growth margins occurs when they meet at (ii) (cf. Taylor 1976, text-fig. 5A). Successive annular growth margins are incorporated into the helico-spiral growth margin extending down the parent branch. C, convergence of annular growth margins from daughter branches. Their inclined nature causes anastomosis to be eccentric.

The colonies are viewed from above the growth tips but angular divergence of daughter branches is ignored for it would obscure parts of the parent branch. Anastomosis between growth margins from two spiral daughter branches apparently caused each to be alternately continuous with the spiral growth margin on the parent branch (text-fig. 13A). Successive annular growth margins were absorbed into the spiral growth margin extending down the other daughter branch and the parent branch (text-fig. 13B), whilst pairs of annular growth margins coalesced at their junction with the parent branch (text-fig. 13C) to form a basally extending annulus on the parent branch.

Secondary or adventitious branching. Secondary branches usually occur near to the zoarial base and consist of a single small branch arising from a larger parent branch at an angle of about 90° (Pl. 34, fig. 6). Both helico-spiral and annular growth margins have been observed on secondary branches. The former are continuous with growth margin on the parent branch, the latter may subsequently anastomose with growth margin on the parent branch. Zoarial sections reveal that secondary branches are not a product of endozonal dichotomy at the growth tip, but are produced at exozonal growth margins by the formation of a secondary endozone approximately perpendicular to and not continuous with the endozone of the parent branch. The inferred sequence of events during formation of a secondary branch are illustrated in text-fig. 14. Firstly, a short length of growth margin became occluded, causing initiation of pivot point-like structures (Taylor 1976) at each end of the occlusion. The growth margin around one of the pivot points broadened (growth stage 'ii') and zooecia began to be formed at divisions of interzooecial walls independent of the budding lamina (i.e. endozonal budding) thus establishing a new endozone. A new series of omega endozonal zooecia formed on the rudimentary secondary branch and extended the budding lamina away from the parent branch with further growth. Frontal walls began to develop (growth stage 'iii') on zooecia of the adventitious branch and eventually exozonal overgrowth commenced.



TEXT-FIG. 14. Inferred formation of an adventitious or secondary branch on the exterior of a *Terebellaria* branch in three growth stages ('i'–'iii'). Full explanation in text. Coarse stipple, non-occluded exozonal growth margin; fine stipple, occluded exozonal growth margin; arrows, inferred growth direction.

The occurrence of secondary branches is usually associated with regions of occluded growth margin near zoarial bases. In some cases large zoaria bear two or more secondary branches diverging in different directions from the parent branch. They appear to owe their origin to localized rejuvenation of growth. In other instances relatively small zoaria, often lacking primary dichotomies, may bear a single secondary branch. These colonies perhaps became detached from their substrate and lay flat on the sea-bed, whereon the adventitious branch formed on the upward-facing side of the colony to renew growth away from the substrate.

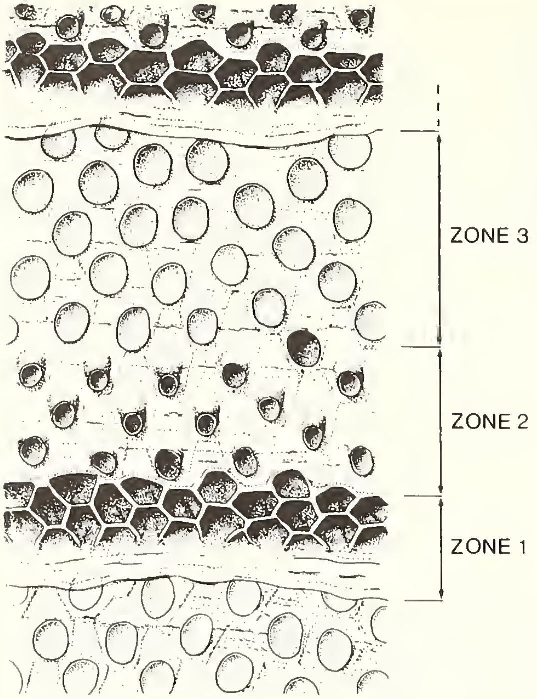
In their relationship with the parent branch, secondary branches are broadly comparable with the 'subsequent-type' branches described from the Palaeozoic cryptostome *Rhabdomeson* (Blake 1976). Subsequent-type branches are thought to have functioned in asexual colony propogation by becoming detached from the parent branch to establish a new 'colony' elsewhere (Blake 1976). Propogation by fragmentation is also known from the cheilostomatous bryozoan *Discoporella umbellata* (Marcus and Marcus 1962) and many colonial anthozoans (e.g. Gilmore and Hall 1976) where it may be of considerable importance during recruitment into new regions. A similar process may have occurred occasionally in *Terebellaria*.

EARLY ASTOGENY

The early parts of colony growth in *T. ramosissima* are poorly known. The smallest zoarium examined (BMNH D52636) has an overgrown ancestrula and some trace of initial frontal wall formation. Zoarial sections prepared from the basal parts of *T. ramosissima* zoaria show that the adnate base rapidly gave rise to an erect stem. Initially the endozone was relatively narrow and the helical trace of exozonal origin was tight. Broadening of the endozone was accomplished by increasing the number of endozonal zooecia budded. Development of young colonies compared with secondary branch formation for these also arose from an adnate lamellar base and subsequently developed endozonal budding independent of the budding lamina.

ZOOIDAL ONTOGENY

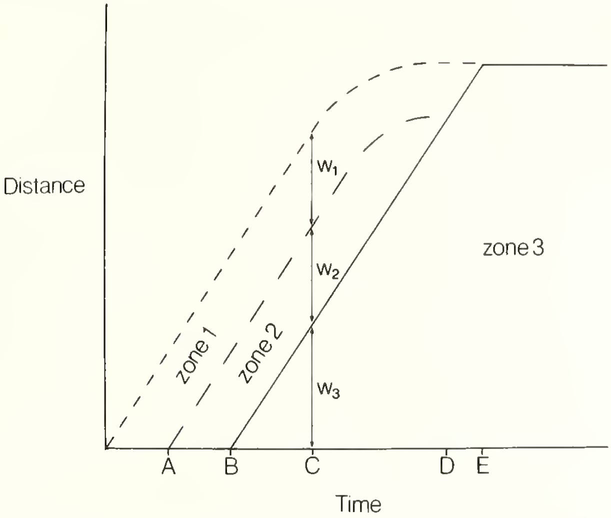
Because older zooids are more distant from the budding region than are younger zooids, bryozoan colonies have an ontogenetic gradient which is directed proximally away from the budding region (Boardman, Cheetham, and Cook 1970). The zooidal ontogeny of *T. ramosissima* is closely comparable to that described for living Diastoporidae (Silén and Harmelin 1974) in which three zones of zooids define distinct stages in an otherwise continuous ontogenetic gradient. Zone 1 is the zooidal budding region or growth margin in which incomplete zooids are enclosed beneath a hypostegal coelom. Zone 2 is composed of zooids which are actively feeding and possess peristomes. Zone 3 comprises zooids which have lost their peristomes and cannot feed because they are sealed by calcareous terminal diaphragms. Skeletal evidence shows that analogous zones existed in *T. ramosissima* colonies during life (Pl. 34, fig. 2; text-fig. 15). Zone 1 is represented by the growth margin and growth tip where zooidal budding occurred and which, by inference, was enclosed within hypostegal coelom. Zooecia having frontal walls, open apertures and peristomes comprise zone 2. As with living Diastoporidae the peristomes of zooecia in *T. ramosissima* colonies increase in height proximally along the ontogenetic gradient. The zooids of zone 2 would have possessed a lophophore and a gut (i.e. a polypide) enabling them to perform a feeding function.



TEXT-FIG. 15. Camera lucida drawing of exozonal zooecia displaying ontogenetic zonation. Zone 1 (the growth margin) is the region of partly formed zooecia. Zone 2 contains zooecia with open apertures and peristomes. In zone 3 zooecia are occluded by terminal diaphragms. The distal fringe of the budding lamina belonging to the growth margin next nearest the branch apex overgrows zone 3; BMNH 11510d, 'Great Oolite, ?locality'. × 28.

An abrupt loss of peristomes and occlusion of zooecial apertures occurs between zones 2 and 3 in *T. ramosissima*. These changes are analogous to those accompanying polypide degeneration in extant Diastoporidae. Gregory (1896*a*, *b*) termed the occluded zooecia of zone 3 in *T. ramosissima* dactylethra, but did not fully understand their ontogenetic significance, interpreting them instead as heterozooecia. The calcareous diaphragms which cover apertures of zone 3 zooecia possess pseudopores, indicating that they are part of a calcified exterior body wall and are equivalent to the terminal diaphragms defined by Nye (1968). Although known from other bryozoan taxa (see Ryland 1970, pp. 59–60), polypide regeneration apparently did not occur in *T. ramosissima*, there being no evidence indicating the necessary resorption of terminal diaphragms proximal to zone 3. Localized absence of zone 2, leaving zone 3 in juxtaposition with the growth margin, is not uncommon in *T. ramosissima*. Occlusion of the growth margin (Pl. 34, fig. 3) by typical calcified exterior body wall (with pseudopores) which completely covers the ends of partly formed zooecia occasionally accompanies absence of zone 2. Loss of the hypostegal coelom and calcification of the terminal membrane (Boardman and McKinney 1976) was probably necessary to occlude the growth margin. If renewed zooidal budding were to occur, the calcified portion of the exterior body wall would first have to be resorbed. Progressive occlusion of growth margin distant from the growth tip occurred in most zoaria examined. Extensive lengths of occluded growth margin may be completely overgrown near the colony base by active growth margin derived from the growth tip at an astogenetically later stage.

Absence of the zone of open zooecia and occlusion of the growth margin can be explained by variations in the relationship between zooidal budding rate (equivalent to the astogenetic or colony growth rate) and the time required for a zooid to reach skeletal maturity (ontogenetic rate). It is thought that variations in the former were probably more pronounced than variations in the latter, and for simplicity the ontogenetic rate has been made constant in text-fig. 16 which explains the relationship between ontogeny and astogeny in *Terebellaria* (and other tubuloporinid cyclostomes).



TEXT-FIG. 16. Time-distance plot explaining the possible relationship between astogeny and ontogeny. The ontogenetic rate (rate at which zooidal structural maturity is reached) is held constant but astogenetic rate (colony growth rate) is allowed to vary. Short dashes, distal edge of the growth margin; long dashes, distal edge of zooecial frontal walls; solid line, line of occlusion. Zone 2 first appears at time A with the formation of the first zooecial frontal walls. Zone 3 appears at time B when zooecial occlusion commences. At time C the width of zone 1 is W_1, zone 2 is W_2, and zone 3 is W_3. The astogenetic rate is made to gradually decrease after time C. As a result zone 2 becomes progressively narrower before disappearing at time D. Zone 1 subsequently becomes occluded and is completely occluded at time E.

Text-fig. 16 is a time-distance graph on which is plotted the position of the most distal part of the growth margin (dependent on astogenetic rate), the position of the most distal frontal wall (marking the zone 1–2 boundary), and the position of the most distal occluded zooecium (related to ontogenetic rate). The origin of the graph represents the first formed part of the colony, the protoecium. From the protoecium the colony expands distally by extension at the growth margin (zone 1) and zone 2 comes into existence at time A when the first frontal wall is formed. Occlusion of zooecia first occurs at time B initiating zone 3. During normal growth, zones 1 and 2 maintain a constant width but zone 3 widens as the colony expands distally. In text-fig. 16 the rate of zooidal budding or astogenetic rate is shown to decrease after time C. Observations show that the growth margin does not narrow significantly suggesting that decrease in astogenetic rate is accompanied by decrease in the rate of advance of the most distal frontal wall. However, the ontogenetic rate, as portrayed by distal expansion of zone 3, is not affected by reduction in astogenetic rate. Consequently, zone 2 narrows until it eventually disappears altogether at time D. Zone 1 subsequently decreases in width as the growth margin becomes occluded until it is fully occluded by time E. In reality, a considerably more complex relationship between astogeny and ontogeny probably existed. Indeed, it is often difficult to make a distinction between morphological variations between zooids due to different ontogenetic states and those due to astogeny (Cook in press).

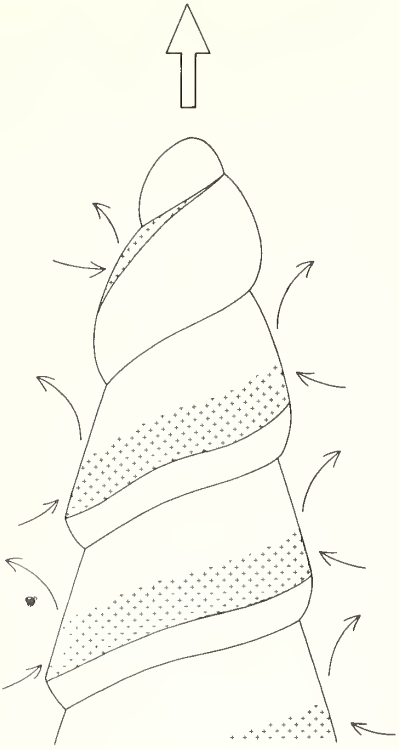
Cessation of zooidal budding near the colony base may have been determined by environmental factors, for example, shortage of food or the presence of muddy sediment at low levels around the colony. Alternatively, it may have related to a decrease in growth vigour dependent on distance from the growth tip and perhaps indicative of hormonal control of growth from growth centres at the branch apices comparable with postulated hormonal control of growth in Palaeozoic trepostomes (Anstey, Pachut, and Prezbindowski 1976).

COLONIAL WATER CURRENTS

The ability of living bryozoan colonies to produce colonial water current systems has recently been recognized (Banta, McKinney, and Zimmer 1974; Cook 1977). Physical co-operation between zooids enables a colonial water current system to be created, probably for a variety of purposes, including enhancement of over-all colony feeding ability, spermatozoan and larval dispersion, and for cleaning the colony surface of sediment. A functional morphological approach (Rudwick 1964) can be applied to fossil zoaria in an attempt to reconstruct colonial water current systems which may have been operative during the life of the bryozoan (e.g. Cowen and Rider 1972). The key premise is that individual zooids in colonies of extinct bryozoans created the same type of feeding currents as those which have been observed from zooids in living bryozoan colonies. In living bryozoans cilia on zooidal tentacles beat to create a current which draws water in at the top of the tentacle crown (Borg 1926, figs. 10–12; Ryland 1970, fig. 6) and passes exhalant water out laterally between the tentacles. Zooids may combine their individual feeding activity to produce currents operating at subcolonial or colonial level. For example, a net exhalant flow has been observed to occur in *Membranipora* sp. over areas of the colony from which zooidal tentacle crowns lean outwards (Banta *et al.* 1974).

It has been inferred that in *T. ramosissima* feeding zooids occupied a band (zone 2) about 1 mm wide immediately proximal to the growth margin. Within this band, peristomes lean towards the growth margin and increase in height away from the growth margin. The inclination of the peristome determines the attitude of the tentacle crown for the tentacle crown itself is too short to lean significantly in cyclostomes (Banta *et al.* 1974). Hence, zooidal lophophores in *T. ramosissima* colonies probably leaned towards the growth margin and were raised gradually higher above the colony surface with increasing distance from the growth margin as peristome height increased

TEXT-FIG. 17. Colonial water current system inferred to have developed along *Terebellaria* branches during life. Small arrows indicate the over-all direction of water flow created by the co-operative action of feeding zooids within zone 2 (indicated by crosses). A distal flow of water exchanged between consecutive bands of feeding zooids may have resulted in a net exhalant flow above the branch apex (large arrow).



towards zone 3. An orientation and distribution of tentacle crowns of this nature would have resulted in a net inhalant flow approaching zone 2 obliquely from the direction of the growth margin (text-fig. 17). The predominant exhalant discharge of water would have been directed towards zone 3 as it rose away from the surface of the colony. The current system would have been repeated several times along each branch, with repetition of the zone of feeding zooids corresponding to each helico-spiral whorl or each annulus. Some exchange of water between zooids in successive bands may have resulted in a general flow of water from the base towards the apex of each branch. Spermatozoan and/or larval dispersion in particular would benefit from expulsion of water over branch tips. The fairly uniform distance maintained between successive whorls or annulae of inferred feeding zooids supports the postulated existence of a colonial water current system during life. The mean distance between whorls or annulae of 2·23 mm (standard deviation = 0·543 mm) determined from 197 measurements made on thirty-five zoaria is similar to known intermonticular distances and distances between exhalant chimneys in *Membranipora* sp. (Banta *et al.* 1974; Taylor 1975).

PALAEOECOLOGY

Despite the abundant preservation of zoarial bases, only rarely are they found adhering to a substratum. Bases of attachment tend to be fairly flat over-all but finely crinkled, with the outermost zooecial layers often inturned at the periphery of the base.

This evidence suggests that most colonies were attached to a perishable (presumably organic) substrate and that inturning of outer zooecial layers may have occurred as a response to decomposition of the substrate.

Colonies from the Bradford Clay of Bradford-on-Avon in Wiltshire are thought to have been a constituent of the fauna associated with the upper surface of a hardground which underlies the clay (Palmer and Fürsich 1974). In Normandy, *Terebellaria* occurs in both cross-bedded oobiosparites and calcareous clays. Colonies probably required environments of stabilized sediment but where current action was sufficient to ensure good water circulation. Their occurrence in clay-rich lithologies may be explained by the often pelleted nature of the clay increasing its coherence and lessening turbidity (Palmer 1974), or by the argillaceous sediment being a later sudden influx. Post mortem breakage and abrasion of zoaria is common, particularly in the Bradford Clay specimens. Zooecial chambers exposed at breakages are sediment-filled rather than calcite-filled, and frontal walls may be worn away. Fractured and worn surfaces may be encrusted by epifauna. Fracturing of colonies often occurred at places where they had been bored into by small lithophagid bivalves. *Terebellaria* zoaria also frequently bear slit-shaped borings, probably made by acrothoracic cirrepeds (Cook 1968, p. 146) and an adnate epifauna dominated by serpulids and bereniciform bryozoans. It seems that most of the attached fauna developed after death of the *Terebellaria* colony, for only rarely is an epifauna immured between exozonal layers. During life, constant overgrowth of the colony surface by successive exozonal layers would have allowed little opportunity for the establishment of an exogenous epifauna. However, regular exozonal layering is occasionally disturbed, possibly by the action of external agencies, and the damage may be covered by subsequent exozonal overgrowth.

In over-all size and proportions, *Terebellaria* zoaria are strikingly similar to the thick branched dendroid cerioporinid cyclostomes abundant in the Bathonian of Normandy. They probably fulfilled a similar ecological role to one another and competed for similar resources. Their similar zoarial forms were, however, produced in distinctly different ways. Cerioporinids retained a hypostegal coelom over their colony surface throughout astogeny and could increase branch diameter by extending existing interzooidal walls. *Terebellaria* achieved the same result of increasing branch diameter by forming a succession of basally directed overgrowths.

SYSTEMATIC DESCRIPTION

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULOPORINA Milne-Edwards, 1838
Family ?DIASTOPORIDAE Busk, 1859
Genus TEREBELLARIA Lamouroux, 1821

Type species. Terebellaria ramosissima Lamouroux, 1821, by monotypy.

Terebellaria ramosissima Lamouroux, 1821

Plates 34, 35; text-figs. 6, 9, 15

1821 *Terebellaria ramosissima* Lamouroux, p. 84, pl. 82, fig. 1.
1821 *Terebellaria antilope* Lamouroux, p. 84, pl. 82, figs. 2–3.
1825 *Terebellaria antilope* Lamouroux; Bronn, p. 20, pl. 6, fig. 13A–B.
1828 *Terebellaria antilope* Lamouroux; Defrance, p. 112, pl. 45, fig. 6.
1830 *Terebellaria ramosissima* Lamouroux; de Blainville, p. 374, pl. 45, fig. 5, 5*a*.
1834 *Terebellaria ramosissima* Lamouroux; de Blainville, p. 409, pl. 67, fig. 5, 5*a*.
1834 *Terebellaria antilope* Lamouroux; de Blainville, p. 409, pl. 67, fig. 6.
1837 *Terebellaria antilope* Lamouroux; Bronn, p. 246, pl. 16, fig. 12A–B.
1845 *Terebellaria ramosissima* Lamouroux; Michelin, p. 231, pl. 55, fig. 10.
1845 *Terebellaria antilope* Lamouroux; Michelin, p. 232, pl. 55, fig. 11.
1850 *Terebellaria tenius* d'Orbigny, p. 318.
1851 *Terebellaria antilope* Lamouroux; Bronn and Roemer, p. 93, pl. 16, fig. 12.
1853 *Terebellaria antilopa* Lamouroux; d'Orbigny, p. 885, pl. 763, figs. 14–18.
1854 *Terebellaria ramosissima* Lamouroux; Haime, pp. 173–175, pl. 6, fig. 12C–I only.
1857 *Terebellaria ramosissima* Lamouroux; Pictet, p. 141, pl. 91, fig. 17.
1881 *Terebellaria ramosissima* Lamouroux; Quenstedt, p. 227, pl. 151, fig. 69.
1896*a* *Terebellaria ramosissima* Lamouroux; Gregory, p. 292.
1896*b* *Terebellaria ramosissima* Lamouroux; Gregory, pp. 188–191, text-figs. 16–17, pl. 10, fig. 5.
1922 *Terebellaria ramosissima* Lamouroux; Canu and Bassler, p. 34, pl. 10, figs. 7–8, 10–19 only.
1952 *Terebellaria ramosissima* Lamouroux; Buge, p. 699, figs. 45–46.
1953 *Terebellaria ramosissima* Lamouroux; Bassler, p. G54, fig. 22, 1A–C.
1967 *Terebellaria ramosissima* Lamouroux; Walter, p. 40, pl. 9, fig. 3.
1968 *Terebellaria tenius* d'Orbigny; Walter, p. 7, pl. A, fig. 9.
1969 *Terebellaria ramosissima* Lamouroux; Walter, pp. 130–132, pl. 8, figs. 6–10; pl. 9, fig. 1.
1972 *Terebellaria ramosissima* Lamaroux; Tavener-Smith and Williams, pp. 132–135, figs. 125–127, 131.

Material. Numerous zoaria from the localities mentioned below, many of which will be deposited in the collections of the BMNH. The following specimens, including all figured material, are from the BMNH collections (supposed localities and horizons are given in Gregory 1896*b*, p. 191; numbers in brackets indicate the number of zoaria per catalogue number):

11510(8), 23857, 24768(2), 24958, 60214, 60215, 60215a–g, 60361, 60382, B163, B2281(5), B4645(3), B4646(5), B4647(3), B4648, B4649, D25(3), D1762, D1812(17), D1823(2), D2110(3), D2111, D2112, D2160, D2165, D2169, D2214, D2240, and 60360(3), B4577(3) 'Bathonian, Ranville'; D1982 'Bradford Clay, ?locality'; D47408 'Jurassic, ?locality'; D52636 Upper Bathonian, Amfreville; D52637 Upper Bathonian, St. Aubin-sur-mer.

Type. According to Walter (1969), Lamouroux's type specimen was destroyed during the destruction of Caen University in 1944. A neotype from the Upper Bathonian of St. Aubin-sur-mer, Normandy was designated by Walter (1969) and is number 28638 in the collections of the Départment des Sciences de la Terre, Lyon.

Revised diagnosis. Tubuloporina with an endozone of erect zooecia which at the branch apices gives rise to a multilamellar exozonal overgrowth of zooecia directed proximally towards the colony base.

Description. Zoaria erect and dichotomously branched. Smaller branches may develop proximal to the zoarial apex, diverging at about 90° from the parent branch. A multilamellar exozone arises from apical growth tips to form a basally directed overgrowth around a cylindrical endozone. The exozonal budding lamina originates where axial interzooecial walls of a particular row of endozonal zooecia (the omega zooecia) divide at the circumference of the endozone. The overgrowth may occur from a helico-spiral growth margin or, less commonly, from a succession of annular growth margins. Endozonal autozooecia are budded interzooecially at triple junctions between previously existing interzooecial walls. The locus of endozonal autozooecial budding occurs above the axial walls of omega zooecia and rotates with zoarial extension. Exozonal autozooecia form at divisions of existing interzooecial walls on a basal budding lamina of exterior body wall. Exozonal autozooecia are rather thinner-walled, more angular in cross-section and have shorter frontal walls than endozonal autozooecia. Autozooecia have short frontal walls, commonly six-sided, with a large, slightly longitudinally elongate aperture situated distally. Long, distally tapering peristomes are lost in later ontogeny and the aperture becomes occluded by a terminal diaphragm bordered by a slightly raised rim. Intrazooecial structures include occasional thin-walled, non-terminal diaphragms and some cystiphragm-like structures. Kenozooecia are infrequent, although some apparent kenozooecia which lack any trace of an aperture occur particularly near the zoarial base. Only a small proportion of zoaria bear ovicells. The ovicell is an inflated gonozooecium which is transversely elongate and has a small, terminal, transversely elongate ooeciopore (Pl. 34, fig. 8).

TABLE 1. Dimensions of exozonal autozooecial characters. Nc, number of colonies considered; Nz, total number of zooecia measured (at least fifteen per colony); $\bar{x}$, mean value in mm calculated by averaging within colony means; SD, standard deviation in mm; CV, coefficient of variation ($100 \times SD \div \bar{x}$); rc, range of colony means in mm; rz, range of zooecial values in mm. Abbreviations for characters given in text-fig. 18.

Character	Nc	Nz	$\bar{x}$	SD	CV	rc	rz
ldw	30	738	0·20	0·018	8·8	0·16–0·23	0·11–0·31
tdw	30	738	0·17	0·012	7·3	0·14–0·18	0·10–0·22
fwl	11	269	0·38	0·096	25·3	0·29–0·55	0·19–0·94
fww	11	269	0·25	0·017	6·8	0·22–0·27	0·18–0·33
law	—	—	*c.* 0·14	—	—	—	—
taw	—	—	*c.* 0·11	—	—	—	—

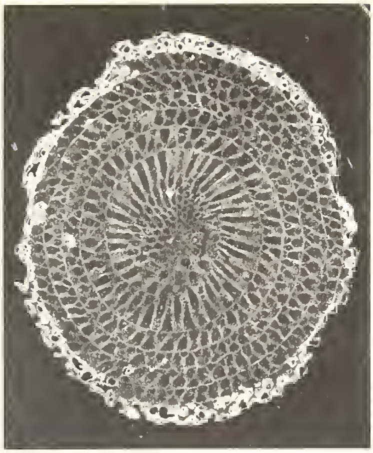
TABLE 2. Dimensions of ovicellular characters. Nc, number of colonies considered; No, number of ovicells measured; $\bar{x}$, mean value in mm calculated by averaging the summed data from all ovicells; SD, standard deviation in mm; CV, coefficient of variation; r, range of values in mm. Character abbreviations; lo, length of ovicell frontal wall; wo, width of ovicell frontal wall; low, longitudinal ooeciopore width; tow, transverse ooeciopore width.

Character	Nc	No	$\bar{x}$	SD	CV	r
lo	11	30	0·88	0·210	24·0	0·48–1·22
wo	11	37	2·01	0·482	24·0	0·99–2·92
low	7	10	0·09	0·024	27·3	0·06–0·13
tow	7	10	0·14	0·035	25·5	0·10–0·20

EXPLANATION OF PLATE 35

Figs. 1–7. *Terebellaria ramosissima* Lamouroux. Bathonian, Ranville. 1, BMNH 60215c, transverse section of branch with sinistral helico-spiral growth margin, × 6·4. 2, BMNH D2111f, longitudinal zoarial section; compare with text-figs. 2A and 7, × 9·5. 3, BMNH D2111d, transverse zoarial section in the vicinity of a branch dichotomy. The uppermost daughter branch displays annular exozonal growth, the lowermost displays spiral exozonal growth, × 6·3. 4, BMNH 60215c(8), endozonal budding on the axial wall of an omega zooecium (arrowed), and the transition between endozone and exozone; compare with text-fig. 6B, × 41. 5, BMNH D2111k, exozonal layers with zooecia cut transversely, × 36. 6, BMNH D2111d, an interzooecial wall with a pore (arrowed) dividing into two zooecial frontal walls overgrown by the basal lamina of a succeeding exozonal layer, × 244. 7, BMNH D2111d, zooecial frontal wall with two pseudopores (lower centre) covered by the basal lamina (arrowed) of a succeeding exozonal layer, × 646.

Figs. 1–3 are negative photographs prepared from acetate peels. Figs. 4, 5 are light photomicrographs of acetate peels. Figs. 6, 7 are scanning electron photomicrographs of an etched specimen.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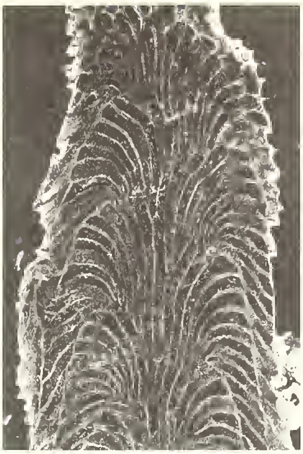
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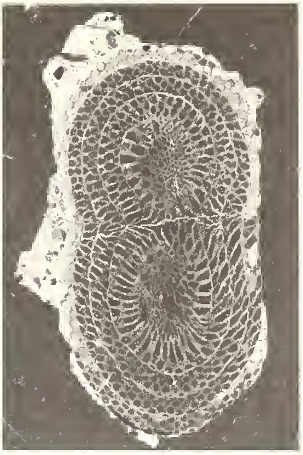
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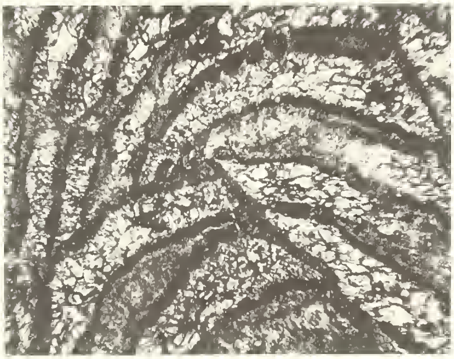
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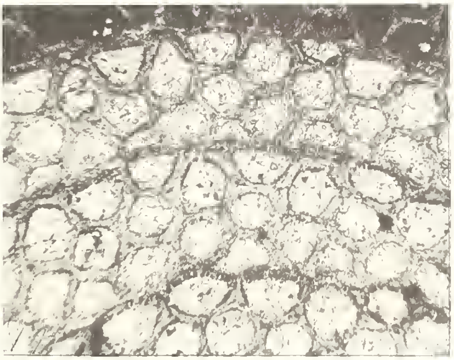
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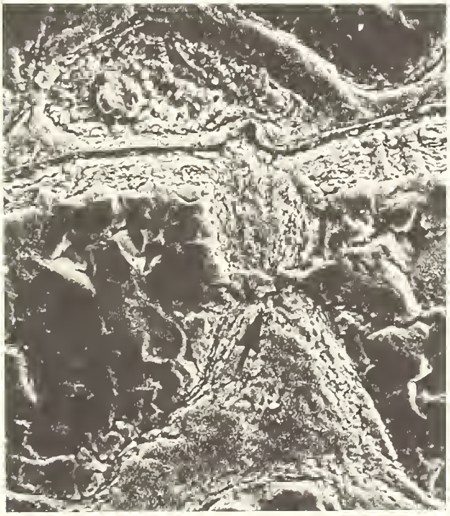
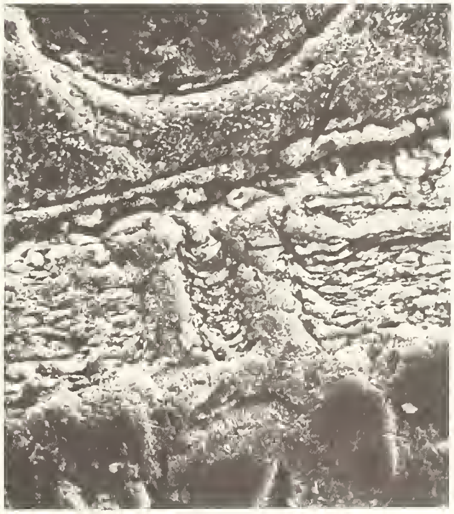

6


7

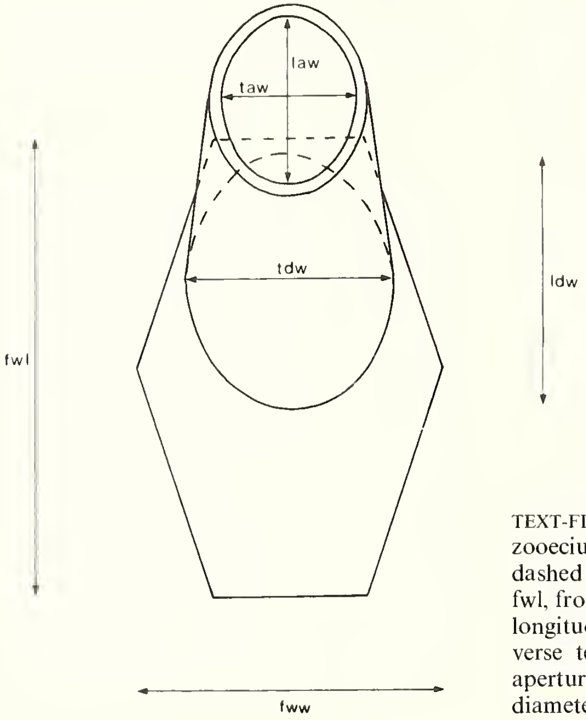
TAYLOR, *Terebellaria ramosissima*

Remarks. As Walter (1969) pointed out, Lamouroux's (1821) two species of *Terebellaria*, *T. ramosissima* and *T. antilope*, are synonymous. *T. antilope*, the junior synonym, was used for slender zoaria, and *T. ramosissima* for zoaria with broad branches. Differences of this nature may be astogenetic (related to colony age) or ecophenotypic, and can be explained by the growth model here proposed.

T. ?increscens Vine, 1884 is probably a form of *Reptomultisparsa microstoma* (Michelin, 1845) (see Walter 1969, pp. 80–81) possessing erect *Pustulopora*-like branches which were subsequently covered by intracolonial lamellar overgrowths, giving the appearance of a multilamellar exozone. The overgrowths do not, however, originate at apical growth tips, and the axial erect portion of the zoarium has a symmetrical appearance in zoarial transverse section, contrasting with that of *T. ramosissima*. Zoarial longitudinal sections reveal, in contrast to *T. ramosissima*, the erect axis of the zoarium and the multilamellar peripheral overgrowths separated by exterior body wall. This form of *R. microstoma* is more abundant than *T. ramosissima* in bradfordian facies deposits of England and probably has been frequently misidentified as *T. ramosissima*, judging from museum collections examined.

Although the suborder Tubuloporina (see Brood 1972, p. 174) is not totally satisfactory as presently understood, *Terebellaria* is provisionally classified with that suborder in accordance with Walter (1969) for the following reasons:

1. A conventional 'single-walled' (Borg 1926) mode of growth (equivalent to stictocystic growth of Ryland 1970, and fused-wall growth of Boardman 1976) is inferred from the presence of typical zooecial frontal walls (Pl. 35, fig. 7) composed of exterior body wall. *Terebellaria* cannot be classified with the two



TEXT-FIG. 18. Diagram of a *Terebellaria ramosissima* zooecium to show the characters measured. Detail is dashed where obscured when a peristome is present. fwl, frontal wall length; fww, frontal wall width; ldw, longitudinal terminal diaphragm width; tdw, transverse terminal diaphragm width; law, longitudinal apertural diameter; taw, transverse apertural diameter.

other single-walled cyclostome suborders Articulata and Salpingina respectively, for it lacks articulating nodes between internodes of zooecia, and does not possess avicularia-like polymorphs or operculate autozooecia.

2. The ultrastructure of the interzooecial walls consisting of a granular layer flanked by laminar layers is of Brood's (1972, p. 33) tubuloporinid type.

3. The ovicell is an inflated gonozooecium typical of tubuloporinidean ovicells.

4. The sequence of ontogenetic changes, apparent from autozooecial characteristics, compares closely with those described from an extant family of tubuloporinideans by Silén and Harmelin (1974).

The suggestion that *T. ramosissima* is a rectanguloid has been made by Tavener-Smith and Williams (1972, p. 135). Their interpretation, however, appears to be founded on an erroneous comprehension of its three-dimensional zoarial form (cf. fig. 131 of Tavener-Smith and Williams with text-fig. 7 here).

Stratigraphical range (according to Walter 1969). Upper Aalenian (*concavum* Zone) to Lower Callovian (*macrocephalus* Zone).

Confirmed occurrence. Southern England. Bathonian: Upper Rags, Great Oolite (*aspidoides* Zone), Bathampton Down, Somerset (ST776653); Forest Marble (*aspidoides* Zone), Fault Corner, Bridport, Dorset (SY453908); Bradford Clay (*discus* Zone), Canal Quarry, Bradford-on-Avon, Wiltshire (ST826600).

Normandy, France. Bathonian (lithostratigraphical divisions and ammonite zones after Palmer 1974): Fontaine-Henry Member (*morrisi* and *subcontractus* zones), Fontaine-Henry (T979786); Blainville Member (*morrisi* to *aspidoides* zones), Blainville (U080731); Campagnettes Member (*aspidoides* Zone), Carriere des Campagnettes Ranville (U114748); St. Aubin Member (*aspidoides* Zone), Amfreville (U121760), Carriere des Campagnettes Ranville (U114748), Reviers (T957818) (considered to be St. Aubin Member rather than Fontaine-Henry Member, Palmer pers. comm. 1976), St. Aubin-sur-mer (T851015); Langrune Member (*discus* Zone, *hollandi* Subzone), Douvres la Deliverande (U032815), Luc-sur-mer (U054850), Commeaux (U228233), Occagnes (U232238).

DISCUSSION

Terebellaria displays a growth form which would appear to be unique amongst bryozoans. No other taxa are known to combine an essentially erect framework with an apically diverging, characteristically spiral, overgrowth. Spiral, or more correctly, helical budding sequences do, however, occur in numerous other erect cyclostomes, e.g. *Spirentalophora* (McKinney 1975), *Spiropora* (Voigt and Flor 1970), and *Zonopora* (Nye 1976). In *Spiropora* some branches have a helical zooecial budding sequence reflected by helical arrangement of apertures on the colony surface, but other branches have a periodic sequence of zooecial budding giving rise to an annular arrangement of apertures on the colony surface. A similar flexibility of growth is displayed by *Terebellaria* in which continuous helical endozonal budding and periodic annular endozonal budding produce branches which have a spiral overgrowth and annular overgrowths respectively in the same colony. This type of intracolony growth variation seems anomalous because other morphological features imply a precise pattern of growth involving considerable colonial co-ordination. The presence of a hypostegal coelom is usually taken to indicate a high degree of colony dominance over individual autonomy (Boardman and Cheetham 1973). Thus a higher degree of colony dominance may be expected within the common bud than in areas away from the common bud. It follows that colonial co-ordination of growth within one particular area of common bud should be greater than colonial control of growth between discrete areas of common bud separated by areas of the colony lacking hypostegal coelom. Hence, discrete common buds may be expected to function semi-autonomously. Therefore, in *Terebellaria*, over-all organization of growth in colonies with a solitary helico-spiral growth margin should have been considerably greater than in colonies with annular growth margins each functioning semi-autonomously.

As in many other animals which secrete an accretionary skeleton (see Gould 1970), the relatively intricate three-dimensional morphology of *Terebellaria* is the product of a few comparatively simple 'rules' of growth. The involved form of *Terebellaria* may be synthesized given that:

1. Axial walls of a row/rows of endozonal zooecia (omega zooecia) which arose nearest to the centre of the endozone functioned as the locus of endozonal budding.
2. The locus of endozonal budding rotated during growth.
3. Axial walls belonging to the row/rows of endozonal zooecia (omega zooecia) which arose nearest to the endozone centre dichotomized into a frontal wall and a budding lamina on meeting the surface of the cylindrical endozone.
4. Previously formed zooecia were overgrown by exozonal zooecia arising on the basally extending budding lamina.

Many unusual morphological features of the zoarium are a necessary consequence of the aberrant growth mode. For example, endozonal zooecia must fill the spaces between successive whorls described by the helical row of omega zooecia, or successive annulae described by consecutive rows of omega zooecia. In order to do so, endozonal zooecia budded further distally within each whorl or annulus make successively greater angles with the zoarial axis (text-fig. 7). The result is that the total length of endozonal zooecia decreases but their frontal wall length increases away from the endozonal axis towards the contiguous exozone. The use of morphological features of this type as independent characters in taxonomic descriptions may therefore be questioned. By applying a more dynamic description of morphology such superfluous characters can be eliminated.

Terebellaria probably possessed a number of functional attributes which would have conferred selective advantage under certain environmental conditions. Multilamellar exozonal growth allowed older portions of the colony lacking feeding zooids to be overgrown by younger portions of the colony with feeding zooids. Moreover, the erect endozonal framework, probably produced at a relatively high cost in terms of energy expenditure, functioned secondarily as a support for subsequent exozonal growth. Thus, a large part of the colony, the exozone, enjoyed the low energy expenditure of adnate growth but gained many of the advantages of erect growth, in particular, freedom from the spatial competitive restrictions of an external substratum. Basally extending exozonal overgrowths strengthened the colony near to the zoarial base where most required, whilst also restricting colonization of the bryozoan by epifauna and boring organisms. A further selective advantage was probably bestowed by the colonial water-current system, which would have enhanced colony feeding efficiency and aided spermatozoan and larval dispersal.

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THE AMMONITE *STOLICZKAIA* FROM THE CENOMANIAN OF ENGLAND AND NORTHERN FRANCE

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ABSTRACT. *Stoliczkaia* Neumayr, 1875, a predominantly Upper Albian genus of world-wide occurrence, is represented in the Lower Cenomanian of England and northern France by a species of the subgenus *S.* (*Shumarinaia*) Matsumoto and Inoma, 1975, and by two species referred to a new subgenus, *S.* (*Lamnayella*) Wright and Kennedy nov. This new subgenus is shown to include the previously described *S. texana* (Cragin), *S. uddeni* Böse, *S. crotaloides* (Stoliczka), and *S. clavigera* Neumayr. *S.* (*Lamnayella*) probably evolved from *S.* (*Stoliczkaia*) by development of juvenile stages with a more markedly fastigiate venter, a feeble siphonal tubercle, middle growth stages with markedly bullate narrow strong ribs which either branch from bullae or are intercalated between primaries, and a mature stage with strong, distant, narrow, predominantly long ribs. It is an independent development parallel to, but distinct from, the contemporaneous *Paracalycoceras* Spath, 1925.

THE genus *Stoliczkaia* was introduced by Neumayr in 1875 for a group of Cretaceous ammonites with ribbed inner whorls and relatively smooth outer whorls. It included species now referred to *Fagesia* (e.g. *Ammonites rudra* Stoliczka) and *Neoptychites* (e.g. *Ammonites telinga* Stoliczka) as well as to *Stoliczkaia* as now conceived.

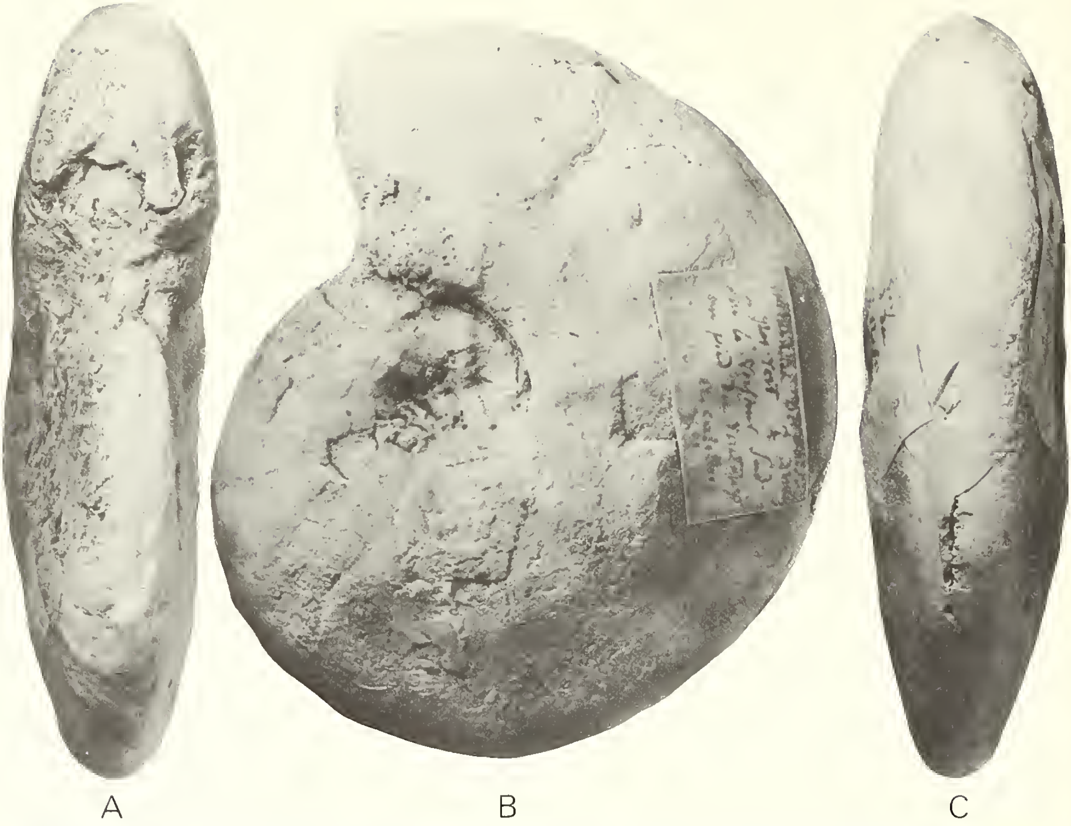
Diener (1925, p. 179) designated d'Orbigny's *Ammonites dispar* as type species and the genus has generally been taken as indicative of a world-wide *Stoliczkaia dispar* Zone at the top of the Albian stage (e.g. Spath 1923*a*, *b*, 1923*c*–1943; Arkell *et al.* 1957). At various times, however, there have been records of the genus in association with Lower Cenomanian fossils, especially in parts of Texas and northern Mexico (e.g. Böse 1927; Adkins 1928) and, more recently, South America (Reyment and Tait 1972, p. 84) and Japan (Matsumoto and Inoma 1975). In all of these areas, precise dating of this pre-eminently Albian genus is difficult due to poor stratigraphical control (e.g. Japan, Brazil) or the endemic nature of associated faunas (Texas and Mexico) and the only records which are placed in the European standard are the *Stoliczkaia* sp. juv. and *Stoliczkaia* sp. nov. recorded by Hancock (1959) from the Cenomanian stratotype and by Kennedy (1969, 1970, 1971) from southern England. These and other recently discovered English and French specimens of Cenomanian *Stoliczkaia* are described below as new species of a new subgenus *S.* (*Lamnayella*) nov. and the recently described *S.* (*Shumarinaia*) Matsumoto and Inoma.

SYSTEMATIC PALAEONTOLOGY

Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family LYELLICERATIDAE Spath, 1921
Subfamily STOLICZKAIINAE Breistroffer, 1953
Genus STOLICZKAIA Neumayr, 1875

Type species. Ammonites dispar d'Orbigny, 1841, by subsequent designation by Diener (1925, p. 179). The holotype of this poorly understood species is figured here photographically for the first time (text-fig. 1).

[Palaeontology, Vol. 21, Part 2, 1978, pp. 393–409, pls. 36–39.]



TEXT-FIG. 1. *a*, *b*. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). Holotype, Renaux Collection, Laboratoire de Paléontologie des Invértébrés, Université des Sciences et Techniques de Montpellier. 'Gres vert-sur le versant du sud au pied de Ventoux'. Original figured by d'Orbigny 1841, pl. 45, figs. 1, 2, × 0·63.

Diagnosis. Small to medium-sized lyelliceratids, typically compressed and moderately involute (although depressed and evolute species are known) with bi- or trituberculate venters when juvenile, ventral tuberculation being lost at an early stage in some species but surviving to maturity in others. Ornament consists of primary ribs, rarely bullate at the umbilical shoulder, separated by one or several shorter intercalated ribs; all the ribs are continuous across the venter. Some species maintain well-developed ribs to maturity; in others the outer whorls are essentially smooth or bear only broad low fold-like ribs.

Occurrence. World wide, Upper Albian and Lower Cenomanian.

Subgenus LAMNAYELLA nov.

Type species. *Stoliczkaia* (*Lamnayella*) *juigneti* sp. nov. Lower Cenomanian, Lamnay, France and Wilmington, Devon, England.

Derivation of name. The subgenus is named from the village of Lamnay in Sarthe, France, source of the majority of the type series.

Diagnosis. Medium sized (adult at *c.* 60 mm) *Stoliczkaia* with fastigiate venter which is feebly trituberculate when young and evenly rounded when mature. Feeble umbilical bullae give rise to single (rarely paired) strong, narrow, high, distant, feebly flexed, prorsiradiate ribs, with from one to three shorter intercalated ribs during early and middle growth. On body chambers, most ribs are long, strong, narrow and distant. The suture has broad, rounded, slightly incised elements.

Discussion. Three subgenera of *Stoliczkaia* have been proposed in addition to the nominate group; typical examples of these are shown in Plates 36, 37, and 39 and text-fig. 1. They may be differentiated from *Lamnayella* as follows: *S.* (*Stoliczkaia*) (text-fig. 1, Pl. 36, figs. 7–9, 12–13), the nominate subgenus, represented by species such as *S.* (*S.*) *dispar* (d'Orbigny) (text-fig. 1, Pl. 36, figs. 12–13) is compressed and involute, with bituberculate inner whorls (Pl. 36, figs. 7–9). Ribbing is low, dense and crowded; ventral tubercles are lost during middle growth (Pl. 36, fig. 13), and the venter becomes rounded. Normally before the beginning of the mature body chamber there is a more or less sudden change in the ribbing; the ribs become more distant and rounded. Thereafter (text-fig. 1), all ornament declines, leaving a smooth body chamber with low broad folds only. Typical species in addition to *S.* (*S.*) *dispar* are *S.* (*S.*) *clavigera* Neumayr, *S.* (*S.*) *undulosa* Breistroffer, *S.* (*S.*) *tenuis* Renz, and *S.* (*S.*) *dorsetensis* Spath.

S. (*Faraudiella*) Breistroffer, 1947 (Pl. 36, figs. 5–6), type species *Ammonites blancheti* Pictet and Campiche, 1859 by original designation. Involute, compressed, with dense, low crowded ribs. Trituberculate venter angular, with siphonal in addition to ventral clavi, which are retained in middle growth stages, although mature body chambers develop low, broad fold-like ribs with only a feeble siphonal tubercle or none surviving. In addition to *S.* (*F.*) *blancheti* (of which *S.* (*F.*) *gardonica* (Hébert and Munier-Chalmas) may be a synonym), *S.* (*F.*) *rhamnonota* (Seeley) is referred to the subgenus as is *S.* (*F.*) *sexangulata* (Seeley) in which ventro-lateral and siphonal tubercles are retained to maturity.

S. (*Shumarinaia*) Matsumoto and Inoma, 1975 (Pl. 38, figs. 19–21), type species *S.* (*Sh.*) *hashimotoi* Matsumoto and Inoma, 1975 by original designation. Very small, evolute, compressed, with ribs sparse, very broad and low, with umbilical bullae and sometimes incipient ventral tubercles; some species develop a tabulate venter with blunt ventral tubercles on the body chamber. *S.* (*Sh.*) *hashimotoi* and *S.* (*Sh.*) *asiatica* Matsumoto and Inoma are diminutive species, adult at less than 40 mm, with greatly reduced sutures. *S.* (*Sh.*) *africana* (Pervinquière) reaches a larger size.

S. (*Villoutreysia*) Casey, 1965 (Pl. 36, figs. 10–11). Type species *S.* (*V.*) *villoutreysi* Casey, 1965 by original designation. Casey differentiated this subgenus by its broad, square venter, strong, persistent ribbing, and generally narrower and shallower umbilicus. On comparing the type species with numerous *S.* (*Stoliczkaia*) from both England and France, we conclude that the features of *S.* (*V.*) *villoutreysi* are of specific significance only. The species is close to *S.* (*S.*) *dorsetensis* Spath.

From these remarks it can be seen that the distinctive features of *S.* (*Lamnayella*) are the evolute coiling, relatively low expansion rate, initially feebly trituberculate but later rounded venter, long and short (rarely branched), distant, sometimes bullate ribs which are retained to maturity and remain sharp, distant, narrow and high even on the mature body chamber. In addition to the type species, the following are referred to the subgenus:

S. (*L.*) *crotaloides* Stoliczka, 1865.
S. (*L.*) *sanctaecatherinae* sp. nov.
S. (*L.*) *tetragona* Neumayr, 1875.
S. (*L.*) *texana* (Cragin, 1893) (of which *S. uddeni* Böse 1927 appears to be a synonym).

In addition we would suggest that *Stoliczkaia* aff. *dispar* Böse (1927, p. 212 (pars.) pl. 5, figs. 1–3) may be a *Lamnayella*.

A number of genera are closely related to *S.* (*Lamnayella*). *Paracalycoceras* Spath, 1925 (type species *Ammonites wiestii* Sharpe, 1857) (Pl. 36, figs. 1–4) has rather similar inner whorls though with more distinct ventral tubercles, but the body chamber bears very characteristic low broad blunt distant rursiradiate ribs, some of which bear strong bullae. These features differentiate it from *S.* (*Lamnayella*) but the genus is presumed to be descended from *Stoliczkaia*, and could well be regarded as no more than a further subgenus of *Stoliczkaia*.

A second Lower Cenomanian descendant of *S.* (*Faraudiella*) is the endemic North American genus *Budaiceras* Böse, 1927 (type species *Budaiceras mexicanum* Böse, 1927 by original designation). Here, however, ribbing is low and flexuous, and there are prominent ventro-lateral and siphonal clavi throughout ontogeny; the latter become twice as numerous as the ribs on the outer whorl.

More problematic are the relationships between *S.* (*Lamnayella*) and *Cottreauites* Collignon, 1929 (type species *Acanthoceras* (*Prionotropis*) *subvicinale* Boule, Lemoine and Thévenin, 1907, by original designation) (text-fig. 2*a*–*c*). This genus is based on pyritic nuclei only and has alternately long and short ribs, sometimes branching from umbilical bullae, with inner and outer ventro-lateral and siphonal tubercles in the type species at least. Collignon (1928–1929) and Sornay (1955) have described a range of other species, some with trituberculate peripheries, others with ventral tubercles and a siphonal keel. Whilst the presence of inner ventro-lateral in addition to outer ventro-lateral and siphonal tubercles suffices to differentiate the type species and thus the genus from *S.* (*Lamnayella*) and other subgenera of *Stoliczkaia*, other species referred to *Cottreauites* may subsequently prove to be nuclei of other species and genera based on larger limestone moulds.

EXPLANATION OF PLATE 36

Figs. 1–4. *Paracalycoceras wiestii* (Sharpe). WW 3556, from the *Mantelliceras saxbii* assemblage Zone fauna of division A2 of the Cenomanian Limestone, White Cliff, Seaton, Devon.

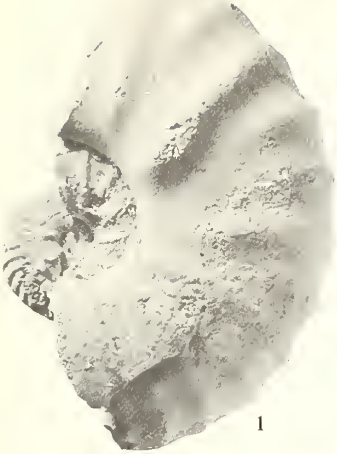
Figs. 5, 6. *Stoliczkaia* (*Faraudiella*) *rhamnonota* (Seeley). Holotype, Sedgwick Museum, Cambridge. From the *Stoliczkaia dispar* Zone fauna of the Cambridge Greensand, Cambridge.

Figs. 7–9. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. U.S. National Museum no. 237003, from the *Stoliczkaia dispar* Zone of Porto Amboin, Angola.

Figs. 10, 11. *Stoliczkaia* ('*Villoutreysia*') *villoutreysi* Casey. Holotype, O. de Villoutreys Collection, Upper Albian, Monte Carlo Tunnel, Monte Carlo.

Figs. 12, 13. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). WW 72344, from the phosphatic fauna of the *dispar* Zone Ammonite Bed, Upper Greensand, White Nothe, Dorset. All figures × 1.

PLATE 36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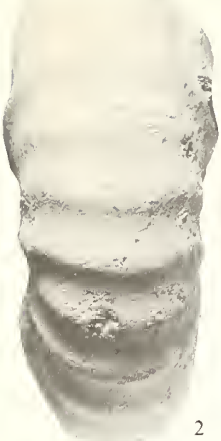
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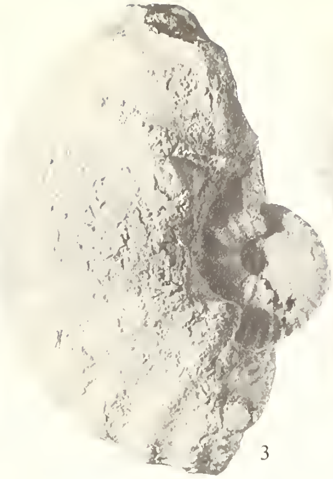
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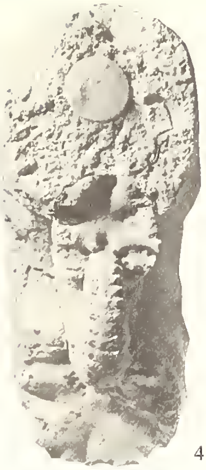
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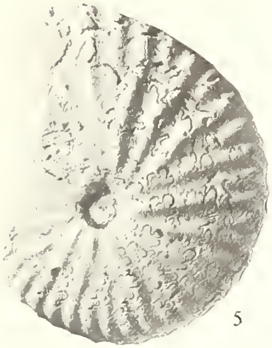
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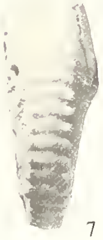
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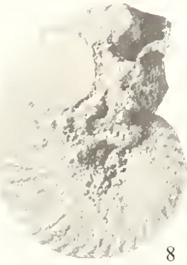
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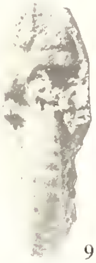
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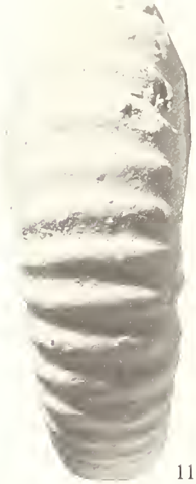
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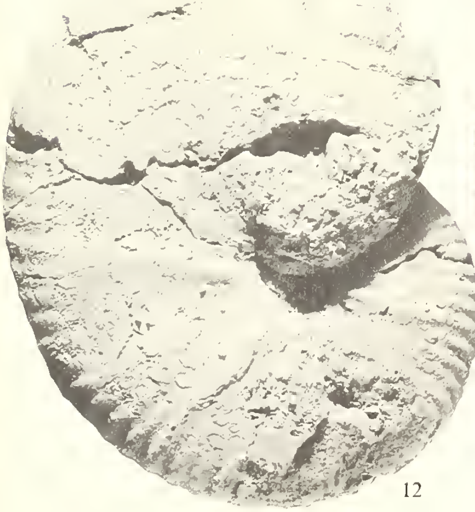
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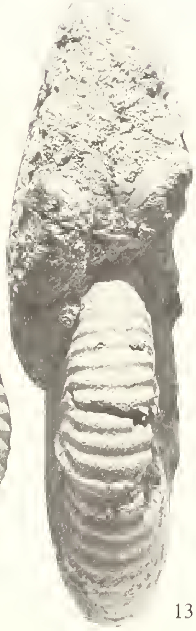
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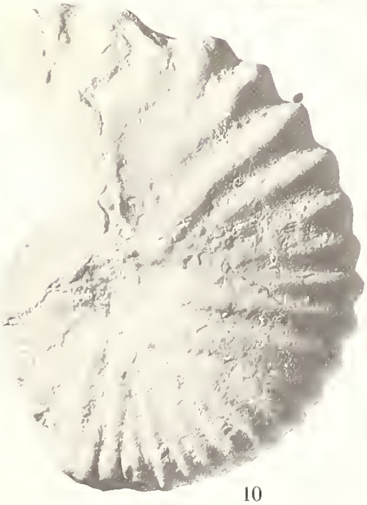
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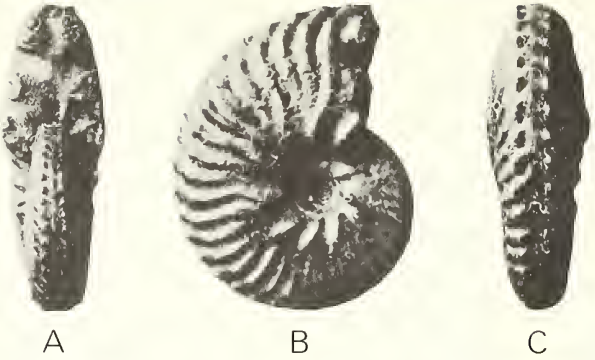
WRIGHT and KENNEDY, ammonoid *Stoliczkaia*



TEXT-FIG. 2. *a–c. Acanthoceras* (*Prionotropis*) *subvicinale* Boule, Lemoine, and Thévenin. Type species of the genus *Cottreauites* Collignon 1929. Copy of Boule, Lemoine, and Thévenin 1907, pl. 8, fig. 5*a–c*, × 2.

Occurrence. S. (*Lamnayella*) is known from England, France, Texas, Mexico, Japan and southern India, and has a proven stratigraphic distribution which extends throughout the western European *Hypoturrilites carcitanensis* assemblage Zone to the base of the succeeding *Mantelliceras saxbii* assemblage Zone, whilst there are questionable fragments from somewhat higher levels. Records elsewhere suggest a restriction to the lower parts of the Lower Cenomanian in Texas and Mexico (Grayson Marl, Del Rio Clay and Buda Limestone). Japanese material comes from a horizon close to the Albian–Cenomanian boundary. The age of the Indian species, which are from Moraviatoor, is not precisely known; they are said to be from the Utatur Group and may be of either late Albian or Cenomanian date. A fragment comparable with the Indian *S.* (*L.*) *crotaloides* has been found in the Upper Albian *Mortoniceras* (*Durnovarites*) *perinflatum* Subzone in Dorset.

Stoliczkaia (*Lamnayella*) *juigneti* sp. nov.

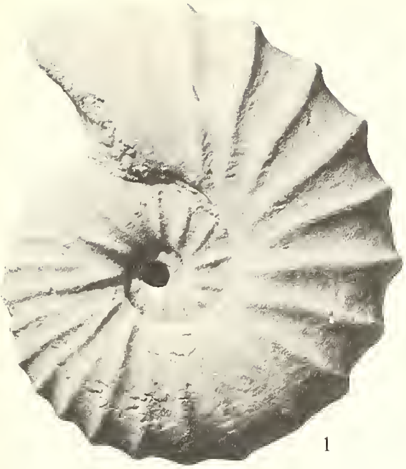
Plate 37, figs. 1–10; Plate 38, figs. 1–12

1959 *Stoliczkaia* sp. nov. Hancock, p. 249.
1971 '*Stoliczkaia*' sp. nov. Kennedy, p. 106.

Types. The holotype is specimen L1 in the Collections of the Muséum d'Histoire Naturelle, Paris, figured on Plate 37, figs. 1–4. Paratypes are L2–L4 and FSM 117 and 173 from the Lower Cenomanian Craie Glauconieuse à *Peten asper* of Lamnay, Sarthe, at the boundary between the *Hypoturrilites carcitanensis* and *Mantelliceras saxbii* assemblage Zones. Paratype WW 15275 is of the same age, and from the Basement Bed of the Wilmington Sands at Hutchin's Pit, Wilmington, Devon (Grid Reference ST 216003; see Kennedy 1970, p. 661 for details).

EXPLANATION OF PLATE 37

Figs. 1–10. *Stoliczkaia* (*Lamnayella*) *juigneti* gen. et. sp. nov. 1–4, the holotype, L1. 5, 6, paratype, FSM 117. 7–10, paratype L3. All specimens from the Lower Cenomanian *Hypoturrilites carcitanensis*-*Mantelliceras saxbii* Zone passage beds, Craie Glauconieuse à *Pecten asper*, Lamnay, Sarthe. All figures × 1.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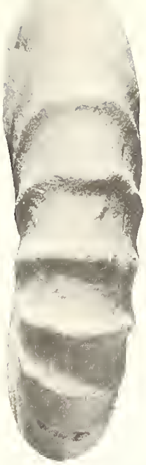
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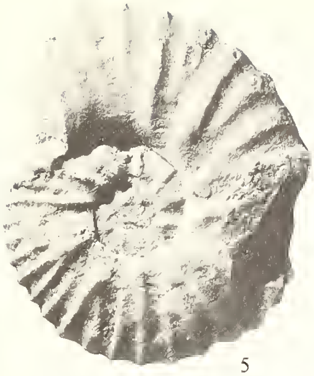
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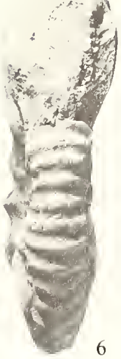
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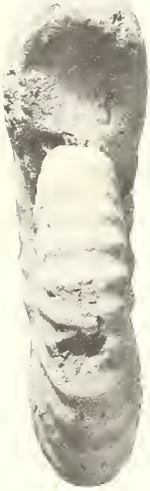
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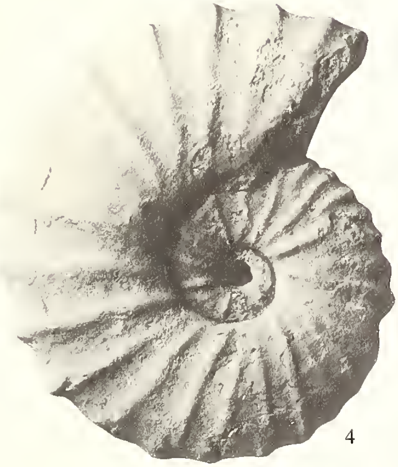
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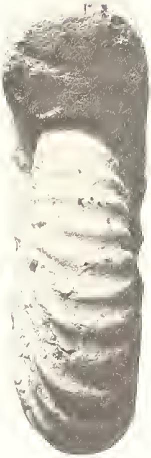
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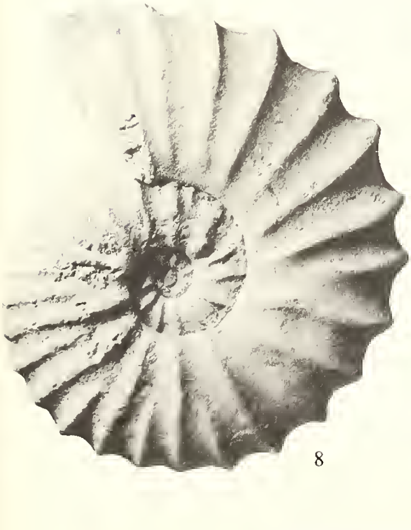
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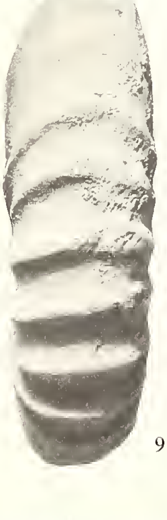
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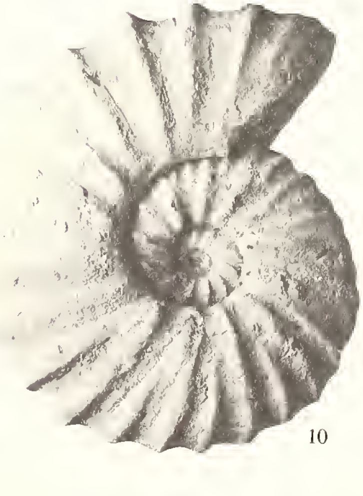
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WRIGHT and KENNEDY, ammonoid *Stoliczkaia*

Derivation of name. The species is named after our good friend Pierre Juignet of Caen who has done so much to clarify the stratigraphy of the Cenomanian of Sarthe.

Dimensions. All dimensions are in millimetres; figures in parentheses are individual measurements as a percentage of diameter. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilical diameter from seam to seam; Ru = ribs at umbilical shoulder; Rt = total ribs; c and ic refer to costal and intercostal measurements respectively.

		D	Wb	Wh	Wb/Wh	U	Ru	Rt
L1	c	61·3(100)	16·2(26)	22·5(37)	72	18·9(31)	19	28
	ic	61·3(100)	14·8(24)	21·5(35)	69	18·9(31)	19	28
L2	c	45·9(100)	13·9(30)	18·1(39)	77	14·0(31)	18	32
	ic	45·9(100)	12·5(27)	16·7(36)	75	14·0(31)	18	32
L3	c	60·4(100)	16·4(27)	23·3(38)	70	19·2(32)	18	29
	ic	60·4(100)	14·4(24)	21·7(36)	66	19·2(32)	18	29
L4	c	40·7(100)	—(—)	17·4(43)	—	10·0(25)	15	30
	ic	40·7(100)	—(—)	16·3(40)	—	10·0(25)	15	30
WW 15275	c	41·7(100)	13·3(32)	14·8(35)	90	9·1(22)	15	—
	ic	41·7(100)	12·6(30)	13·3(32)	94	9·1(22)	15	—

Diagnosis. A compressed, parallel-sided *Lamnayella* with a feebly trituberculate venter up to the middle growth stages, bearing 28–32 ribs per whorl. There are fifteen weakly bullate primary ribs with one to three shorter intercalated ribs during middle growth and long distant ribs only on the adult body chamber.

Description. The holotype and other paratypes from Lamnay are all distorted composite moulds. Only the Wilmington paratype is undeformed, and this retains traces of recrystallized shell. During middle growth the coiling is moderately evolute, with approximately 40% of the previous whorl being covered; at maturity the degree of evolution increases, the last part of the body chamber being markedly eccentric (Pl. 37, figs. 1, 4, 8, 10). The umbilicus is shallow and of moderate breadth (dimensions above) with a low wall and broadly rounded shoulder.

EXPLANATION OF PLATE 38

Figs. 1–12. *Stoliczkaia* (*Lamnayella*) *juigneti* subgen. et sp. nov. 1–3, paratype L4. 4–7, paratype L3, both from the Lower Cenomanian *Hypoturrilites carcitanensis–Mantelliceras saxbii* Zone passage beds, Craie Glauconieuse à *Pecten asper*, Lamnay, Sarthe. 8–12, paratype WW 15275, of the same age, from the Basement Bed of the Wilmington Sands, Hutchin's Pit, Wilmington, Devon.

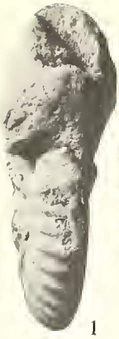
Figs. 13–16, 22, 23. *Stoliczkaia* (*Lamnayella*) *sanctaecatherinae* gen. et. sp. nov. 4*a–d*, the holotype, WW 9863 and 7*a*, *b*, paratype WW 9887, both from the phosphatic Lower Cenomanian *Hypoturrilites carcitanensis* assemblage Zone fauna of the Glauconitic Marl at Rocken End, Gore Cliff, Isle of Wight, Hampshire.

Figs. 17, 18. *Stoliczkaia* (*Shumarinaia*) cf. *asiatica* Matsumoto and Inoma. J. M. Hancock Collection, no. CC 451, from the Lower Cenomanian *Mantelliceras saxbii* Zone fauna of the Marnes de Ballon exposed 3·35 km east of Ballon, Sarthe, France.

Figs. 19–21. *Stoliczkaia* (*Shumarinaia*) *asiatica* Matsumoto and Inoma. Holotype, Geological Collections, Kyushu University, no. TKD 30173A, from the Middle Yezo Group of Shumarinai, Hokkaido, Japan.

Figs. 1–16, 22, 23, × 1; figs. 17–21, × 2.

PLATE 38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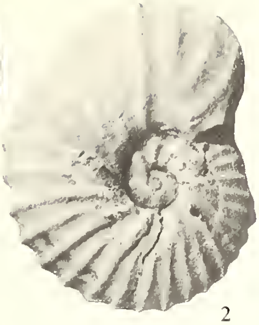
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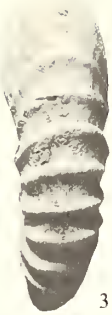
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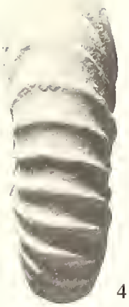
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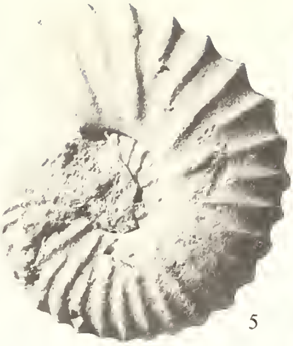
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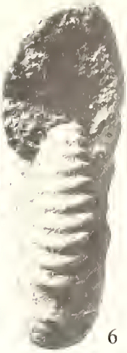
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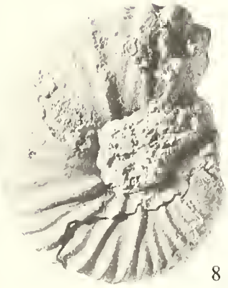
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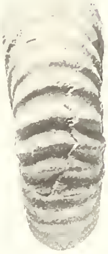
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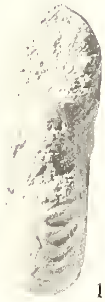
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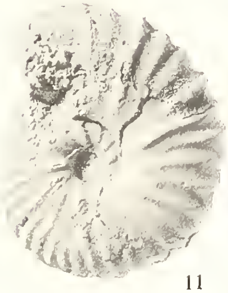
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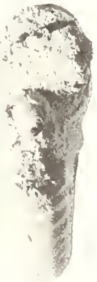
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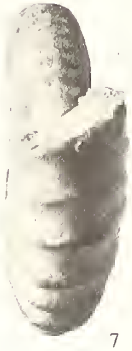
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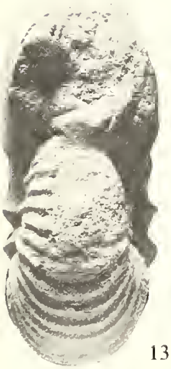
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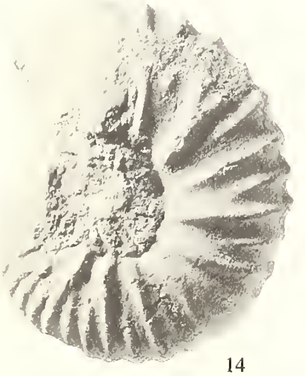
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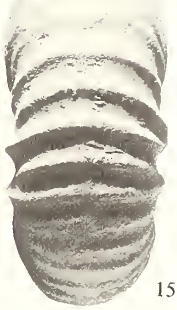
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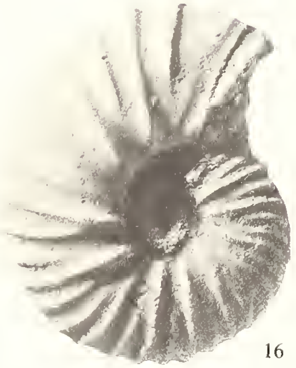
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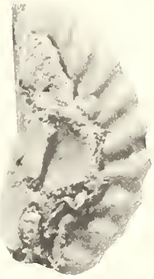
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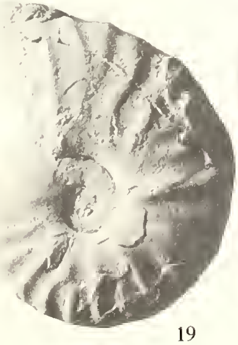
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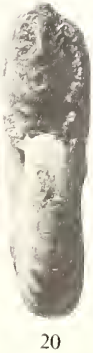
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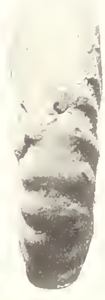
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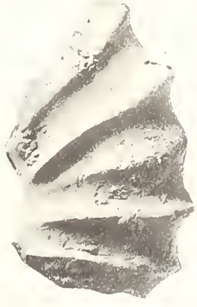
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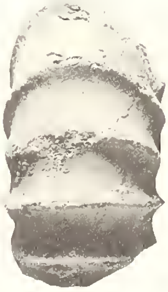
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WRIGHT and KENNEDY, ammonoid *Stoliczkaia*

The whorl section is a compressed oval. The greatest breadth is low on the inner flank in intercostal section and at, or just outside, the bulla in costal section. The inner flanks are broadly rounded and the outer flanks converge to a venter which is narrowly rounded in intercostal section, without distinctly demarcated shoulders, and weakly fastigate in costal section during early growth stages, but rounded later.

Fifteen to eighteen ribs of variable strength arise at the umbilical seam and pass straight up the low umbilical wall. Feeble umbilical bullae of variable strength are present (cf. Pl. 37, fig. 5 and Pl. 38, figs. 7, 11) giving rise to one rib, or rarely a pair (Pl. 37, fig. 5). The ribs are prorsiradiate, narrow, acutely rounded, straight on the inner flank, but gently flexed from mid flank (Pl. 37, figs. 1, 4), projected slightly forwards (and as a result weakly concave) over the outer flank, strengthening to cross the venter with a faint but distinct convex flexure. Between these long ribs are from one (typically) to three (exceptionally) shorter intercalated ribs, most arising some way below mid flank and sometimes tenuously linked to a bulla or to the umbilicus by faint striae. Initially weak, these ribs strengthen across the outer flank, following a similar course and of similar elevation to that of the primary ribs when traced across the venter.

Up to 25–30 mm diameter, the venter is distinctly if weakly fastigiate (Pl. 38, figs. 6, 7, 10, 12), with a ventro-lateral angulation and poorly defined tubercles, much weaker than the faint siphonal tubercle. These suggest a distinctively trituberculate juvenile stage (our specimens do not show the development at less than 20 mm diameter). From approximately 30 mm onwards the venter is evenly rounded and from 40 mm onwards the primary ribs dominate, becoming distant, high and narrow, with bullae declining markedly, so that ribs are connected to the umbilicus by little more than striae in some cases (Pl. 37, fig. 1). At the mature aperture, ribbing weakens and the last few ribs are crowded (Pl. 37, figs. 1, 4, 8, 10).

Only the Wilmington paratype shows the suture line, which is incompletely exposed. It is rather simple with broad, little-incised bifid elements.

Discussion. Compressed whorl section, alternation of long and short ribs during middle growth and dominance of long ribs at maturity separate *S.* (*L.*) *juigneti* from *S.* (*L.*) *sanctaecatherinae* sp. nov., described below, and *S.* (*L.*) *tetragona* Neumayr (text-fig. 3*a*, *b*). *S.* (*L.*) *crotaloides* Stoliczka (text-fig. 3*c*–*e*) has mainly long ribs, which are distinctively flexuous, and a curious middle growth stage with a tabulate venter and looped ribs. *S.* (*L.*) *texana* (Pl. 38, figs. 1–8) is the closest species, but it is more robust, has a higher expansion rate and predominantly long ribs during middle and later growth, the ribs recti- to rursiradiate and convex, rather than prorsiradiate and concave as in our species.

Occurrence. S. (*L.*) *juigneti* is known only from the boundary beds between the *Hypoturrilites carcitanensis* and *Mantelliceras saxbii* assemblage zones of Lamnay, Sarthe, France, and Wilmington, Devon, England.

Stoliczkaia (*Lamnayella*) *sanctaecatherinae* sp. nov.

Plate 38, figs. 13–16, 22, 23; Plate 39, figs. 9–11; text-fig. 4*a*–*c*

pars 1969 '*Stoliczkaia*' spp., Kennedy, p. 467.
1970 Lyelliceratidae gen. et. sp. nov., Kennedy, p. 622.

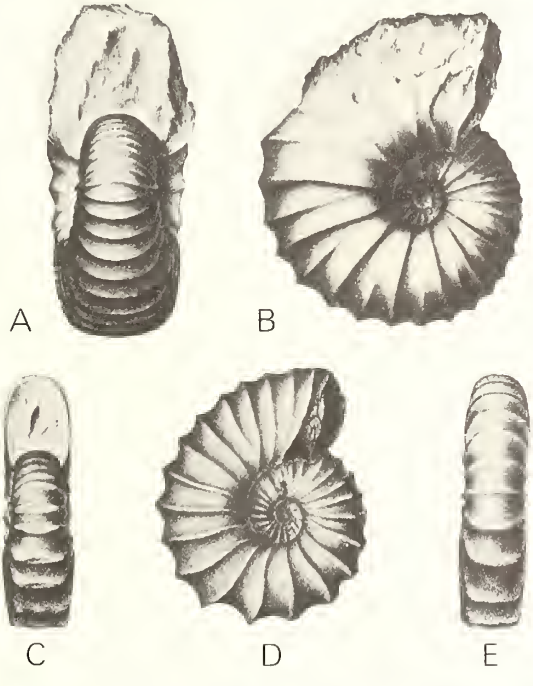
Types. The holotype is WW 9863, from the phosphatic fauna of the Glauconitic Marl exposed in fallen blocks at Rocken End, below Gore Cliff, Isle of Wight, Hampshire (SZ 492755; see Kennedy 1969, p. 525 for details), as is paratype WW 9887; paratype OUM K4787 is from the same horizon at Head Ledge, Eastbourne, Sussex (TV 595955; see Kennedy 1969, p. 506 for details); paratype OUM K4788 is from the same horizon at Stour Bank, near Blandford Forum, Dorset (ST 846106; see Kennedy 1970, p. 622 for details). Two additional specimens tentatively referred to the species are OUM K4789–4790 from the unphosphatized fauna of the Glauconitic Marl at Beddingham Limeworks near Lewes, Sussex (TQ 440073; see Kennedy 1969, p. 50 for details). All specimens are of Lower Cenomanian, *Hypoturrilites carcitanensis* assemblage Zone age.

Derivation of name. From St. Catherine's Point, source of the holotype.

Dimensions.

		D	Wb	Wh	Wb/Wh	U	Ru	Rt
WW 9863	c	47·7(100)	20·3(43)	18·8(39)	1·08	12·9(27)	14	35
	ic	47·7(100)	18·9(40)	17·7(37)	1·07	12·9(27)	14	35

Diagnosis. An inflated *Lamnayella* with fastigiate trituberculate venter during early growth. Middle growth stages have strong umbilical bullae giving rise to groups of two or three strong, narrow, high, distant prorsiradiate ribs which loop across the flanks and venter. Additional intercalated ribs are also present. Ribbing simplifies on the mature body chamber.



TEXT-FIG. 3. *a*, *b*. *Stoliczkaia* (*Lamnayella*) *tetragona* Neumayr. Copy of Stoliczka 1865, pl. 45, fig. 2–2*a*, ×0·5. *c–e*. *Stoliczkaia* (*Lamnayella*) *crotaloides* (Stoliczka). Copy of Stoliczka 1865, pl. 46, fig. 3–3*b*, ×0·5.

Description. The holotype and paratypes are all phosphatic internal moulds. The early stages, at a diameter of approximately 15 mm, are shown by OUM K4788 (Pl. 39, figs. 12, 13). The whorl section is compressed with rather flattened convergent flanks and a fastigiate venter. Ornament consists of both primary and intercalated ribs, all of which bear distinct ventral clavi, connected across the venter by a broad convex rib, which bears a feeble siphonal tubercle.

At an estimated diameter of 25 mm this juvenile morphology has changed, and in middle and later growth stages (Pl. 38, figs. 13–16) ventral tuberculation is lost. The coiling is quite evolute, becoming increasingly so at maturity (Pl. 38, figs. 14, 16). The umbilicus is moderately deep and wide (27% of diameter). The umbilical wall is of moderate height, rounded and with an evenly rounded shoulder. The whorl section is slightly depressed, with the greatest breadth at the umbilical bullae in costal section and just below mid flank in intercostal section. The inner flanks are somewhat swollen; the outer flanks converge to a broadly rounded and somewhat flattened venter. There are fourteen umbilical bullae per whorl, most of them high and narrow, giving rise to groups of two or three ribs, which separate from the bulla on the inner third of the flank. There are also occasional weaker bullae giving rise to a single rib, and some non-bullate ribs which extend almost to the umbilicus as mere striae, whilst there may also be one or two shorter intercalated ribs inserted between long ribs, arising low on the flank. All ribs are prorsiradiate, narrow, high and distant, with a slight forwards projection and concavity on the outer flank, strengthening and broadening across the venter which they pass straight across or with slight convex curvature. Groups of long ribs generally loop between bullae (Pl. 38, fig. 15); in general, the central rib of groups of three or the front rib of pairs arising from bullae is the strongest.

Towards the aperture of the holotype the whorl contracts markedly and the ribbing simplifies, suggesting it to be close to maturity; in paratype WW 9887, a body chamber fragment, the whorls are slightly compressed (coastal Wb: Wh = 0·9) (Pl. 38, figs. 22–23).

The suture is simple, with broad, rounded, little-incised elements.

Discussion. The available material shows some variation in whorl section and coarseness of ribbing, but the species is characterized by the distinctive style of ribbing and the strong bullae, which serve to distinguish it from the more slowly expanding *S.* (*L.*) *juigneti* sp. nov., in which the bullae are weak and generally give rise to simple ribs only. *S.* (*L.*) *texana* (Pl. 39, figs. 1–8) also lacks strong bullae and grouped ribs, having an oval whorl section, a predominance of alternately long and short ribs in youth, and

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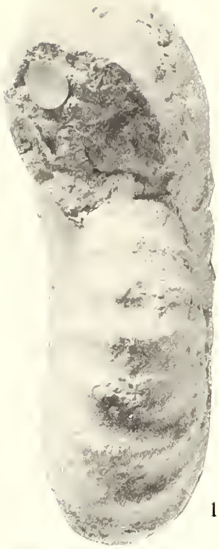
EXPLANATION OF PLATE 39

Figs. 1–8. *Stoliczkaia* (*Lamnayella*) *texana* (Cragin). 1–3, lectotype, Texas Memorial Museum, Austin, no. 19731. 4–6, no. 19740a. 7–8, no. 19740b; probable paralectotypes, all from the 'Vola Limestone' of Denton County, Texas (Grayson Marl or Buda Limestone: Lower Cenomanian).

Figs. 9–13. *Stoliczkaia* (*Lamnayella*) *sanctaecatherinae* gen. et. sp. nov. Paratype OUM K4788, from the Lower Cenomanian *Hypoturrilites carcitanensis* assemblage Zone phosphatic fauna of the Glauconitic Marl at Stour Bank, Dorset.

Figs. 1–11, × 1; 12–13, × 3.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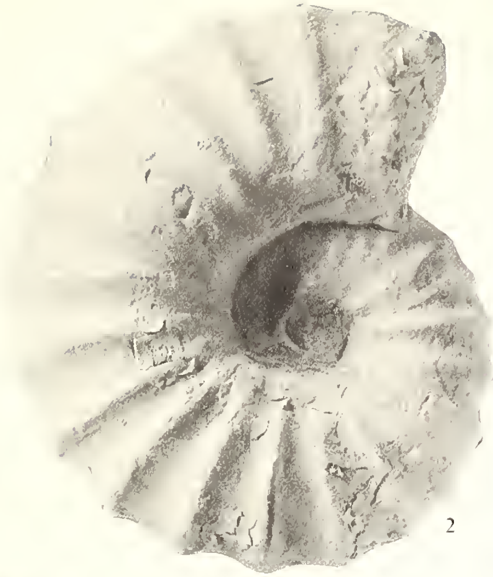
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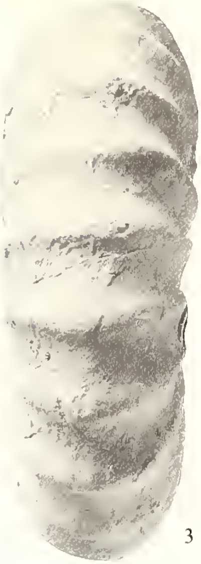
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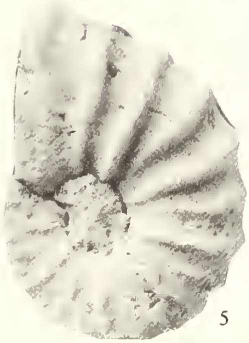
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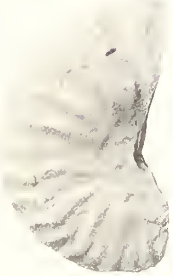
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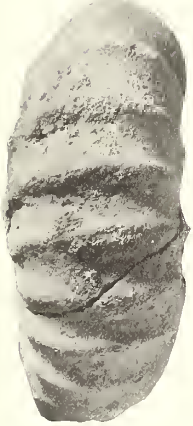
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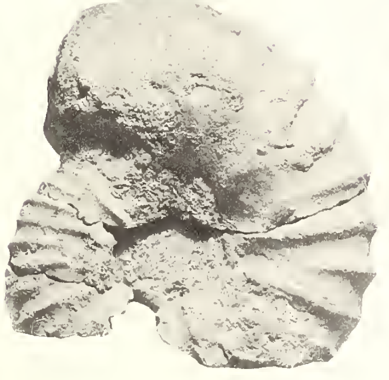
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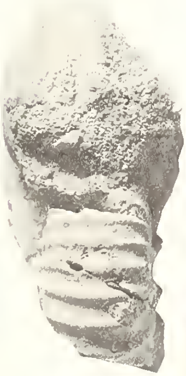
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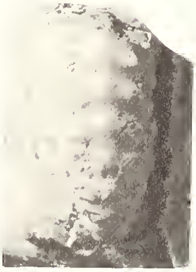
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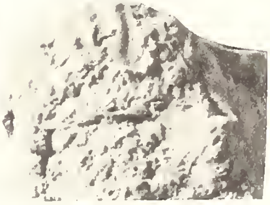
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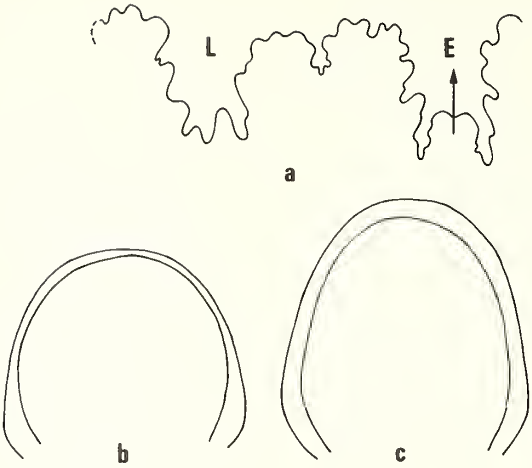
WRIGHT and KENNEDY, ammonoid *Stoliczkaia*



TEXT-FIG. 4. *Stoliczkaia* (*Lamnayella*) *sanctaecatherinae* sp. nov. *a*, partial external suture × 3, and *b*, whorl section × 1·5, of the holotype, WW 9863; *c*, whorl section of paratype, WW 9887, × 1·5.

simple feebly convex rursiradiate ribs during later growth. *S.* (*L.*) *crotaloides* (text-fig. 3*c*–*e*) also has predominantly simple flexuous flank ribs, typically lacks bullae, and has a curious tabulate venter with incipient looping in middle growth. In *S.* (*L.*) *tetragona* (text-fig. 38*a*, *b*), the most similar species, there is also looping of ribs, but the Indian species lacks bullae, has a quadrate whorl section and faintly rursiradiate convex ribs rather than the prorsiradiate feebly concave ribs of our species. The ventral ribs are thin and straight or concave in *S.* (*L.*) *tetragona* rather than thickened and convex as in our form.

Occurrence. The species is known only from the Lower Cenomanian *Hypoturrilites carcitanensis* assemblage Zone of Dorset, Hampshire, and Sussex, England.

Stoliczkaia (*Lamnayella*) sp.

Material. Seven unregistered specimens from the Marnes de Ballon, tranchée de la Gare, Montmirail, Sarthe, preserved in the collections of the Sorbonne.

Remarks. These seven fragments belong to an *S.* (*Lamnayella*) with an oval whorl section and long primary ribs separated by up to three intercalated ribs. They are too poor for fuller determination, but are closest to *S.* (*L.*) *juigneti.*

Occurrence. Lower Cenomanian, high *H. carcitanensis* or low *M. saxbii* assemblage Zone, Montmirail, Sarthe, France.

Subgenus SHUMARINAIA Matsumoto and Inoma, 1975

Stoliczkaia (*Shumarinaia*) cf. *asiatica* Matsumoto and Inoma

Plate 38, figs. 17–18

1959 *Stoliczkaia* sp. juv. Hancock, p. 249.
1971 *Stoliczkaia* sp. juv. Kennedy, p. 106.
cf. 1975 *Stoliczkaia* (*Shumarinaia*) *asiatica* Matsumoto and Inoma, p. 279, pl. 39, figs. 4–7; text-fig. 11.

Holotype. TKD 30173A, in the collections of the Department of Geology, Kyushu University, and from the Late Albian or early Cenomanian part of the Middle Yezo Group of Shumarinai, Hokkaido, Japan.

Material. One specimen only, CC 451, in J. M. Hancock's collection from the Marnes de Ballon exposed in a ditch alongside the Ballon to Bonnetable Road, 3·35 km east of Ballon, Sarthe, France, and of Lower Cenomanian, low *M. saxbii* assemblage Zone age.

Description. The specimen is a composite mould of the body chamber of a small ammonite with an estimated maximum whorl height of 8 mm. The whorl section is compressed, with flattened parallel sides and a venter which is feebly fastigiate at the smaller end of the specimen and flattened at the larger. Ornament consists of blunt prorsiradiate ribs which are convex on the outer flank (the inner flanks are not preserved), thicken as they cross the venter and show distinct convex curvature. At the smallest diameter visible there are poorly defined ventral swellings.

Traces of the inner whorls are preserved as an external mould in the dorsum of the specimen; the whorls seem to have been flat-sided, compressed, with tiny ventral tubercles, giving the nucleus a 'submantellicerine' appearance.

Discussion. This tiny scrap was listed by both Hancock (1959) and Kennedy (1971) as *Stoliczkaia* sp. juv. Its affinities are clarified by the description of *S.* (*Shumarinaia*) by Matsumoto and Inoma (1975). It most closely resembles *S. asiatica* Matsumoto and Inoma, as can be seen from the holotype, refigured here as Plate 38, figs. 19–21. It differs chiefly in the more obviously differentiated ventral tubercles, but Japanese topotypes we have studied show this to be a somewhat variable feature in the species. *S.* (*Sh.*) *africana* (Pervinquière) and *S.* (*Sh.*) *hashimotoi* Matsumoto and Inoma are both more coarsely and robustly ornamented.

Occurrence. S. (*Sh.*) *asiatica* was originally described from the Middle Yezo Group of Hokkaido, Japan, where the age was no more precisely known than Uppermost Albian or Lower Cenomanian. The Sarthe specimen is of definite Lower Cenomanian age.

DISCUSSION

Descriptions of *S.* (*L.*) *juigneti* subgen. et sp. nov., *S.* (*L.*) *sanctaecatharinae* sp. nov., and *S.* (*Shumarinaia*) cf. *asiatica* Matsumoto and Inoma place records of *Stoliczkaia* from the European Cenomanian on a firm basis. They also clarify the age of the Japanese material, the date of which is not precisely defined.

Reference of *S. texana* (Cragin) and the related (if not conspecific) *S. uddeni* Böse to the subgenus further supports the view that the *Graysonites*-bearing strata which yield these species in Texas, Mexico and Japan are of Cenomanian rather than Albian age; unfortunately the evidence is still insufficient to correlate this level firmly with the European standard and to show whether or not it predates the earliest Cenomanian ammonite faunas of Europe (Kennedy 1971; Kennedy and Hancock 1977).

S. (*Shumarinaia*) is known definitely from the Upper Albian and Cenomanian. Accurately dated *S.* (*Lamnayella*) are all of Lower Cenomanian age, and it remains to suggest their evolutionary origins. The fastigiate, feebly trituberculate periphery of juvenile *Lamnayella* suggests that *Faraudiella* may be the ancestor, but this subgenus bears clearly defined clavi, rather than the blunt, poorly defined ventral tuberculation of *Lamnayella*. It seems more likely that *Lamnayella* arose from *Stoliczkaia* sensu stricto, some species of which have fastigiate venters (e.g. Renz 1968, pl. 7, fig. 4*a*, *b*) which, with slight siphonal strengthening would produce the poorly defined or incipient siphonal tubercle of the present form. Furthermore, the ribbing pattern of *S.* (*Stoliczkaia*) of the *dorsetense* and *notha* groups (e.g. Spath 1923*c*–1943, pl. 32, fig. 7; Renz 1968, pl. 6, figs. 5*a*, *b*, 8*a*, *b*), if strengthened and maintained to maturity would closely resemble that of *Lamnayella*.

The small size of adult *Lamnayella* and also of *Shumarinaia* compared with *S.* (*Stoliczkaia*) forces one to consider whether these former may not be microconchs of the latter. However, *Lamnayella* and *Shumarinaia* both range from Upper Albian into Cenomanian whereas, to the best of our knowledge, typical *S.* (*Stoliczkaia*) do not. The balance of evidence at present is that *Shumarinaia* is a genuine dwarf offshoot and *Lamnayella* a small derivative of *S.* (*Stoliczkaia*) that persisted after the extinction of typical forms of the genus.

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TEREBRATULACEA FROM THE CRETACEOUS SHENLEY LIMESTONE

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ABSTRACT. The Lower Albian Shenley Limestone occurs very locally in Bedfordshire, England. The environment of deposition is discussed and it is shown that the rich brachiopod fauna is preserved as slightly disturbed life-assemblages. Terebratulacean hinge plates are shown to consist, in general, of two parts, here called 'primary' and 'secondary' hinge plates; hinge plate terminology is revised. A calcareous structure attached to the dorsal side of the brachidium is described for the first time and named the 'sub-loop skirt'. Systematic descriptions are given of four genera, six species, and two subspecies. Two genera are new: *Boubeithyris* and *Walkerithyris*. Four species and the two subspecies are new: *B. buzzardensis*, *W. mendax*, *Rectithyris shenleyensis*, *R. shenleyensis heathensis*, *Platythyris diversa*, and *P. diversa rubicunda*. The Shenley Limestone terebratulacean fauna is demonstrated to be in many respects transitional between the Aptian and Cenomanian faunas.

THE Lower Albian (Cretaceous) Shenley Limestone of Bedfordshire, England, contains a rich and diverse fauna of which brachiopods are a major part. The Terebratulacea are particularly important as they represent practically the entire known English Albian terebratulacean fauna. In other English Albian beds, the Gault and Upper Greensand, Terebratulacea are sparse, and although the Red Chalk contains a considerable number of brachiopods they represent few species.

The stratigraphical and evolutionary position of the Shenley Limestone Terebratulacea has caused some controversy in the past. Lamplugh and Walker (1903) described the then newly discovered Shenley Limestone fauna and compared it with the Belgian Tourtia fauna described by d'Archiac (1847). The superficial similarity between the two led Kitchin and Pringle (1920) to their 'overturn hypothesis' in which they attempted to show that the limestone bed was of Cenomanian age and that the succession at Shenley was inverted. Lamplugh (1922), however, showed that the bed was of Albian age and this has since been confirmed by ammonite evidence (Wright and Wright 1947). Since the brief description by Lamplugh and Walker (1903) the Terebratulacea of the Shenley Limestone have not been systematically described and there remains a gap in our knowledge of the English Cretaceous Terebratulacea between the work of Middlemiss (1959) on the Aptian fauna and the work of Sahni (1929) on the Chalk fauna. The absence of modern work on the Albian Terebratulacea is more noticeable because E. F. Owen has described other brachiopod groups (1959, 1962, 1963; Owen and Thurrell 1968).

The species described in this paper are all from the Shenley Limestone except *Platythyris capillata* (d'Archiac) from the Tourtia of Belgium and *P. diversa rubicunda* sp. nov. from the Red Chalk, which are included for completeness. In addition to the described species, others occur uncommonly in the Shenley Limestone, but the available material is considered insufficient for a systematic description. A few specimens of a species of *Sellithyris* have been found which is similar in external features to *S. sella* from the English Aptian and has similar internal structure.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 411–441, pls. 40–42.]

Lamplugh and Walker (1903) figured a biplicate terebratulid from the Shenley Limestone as *Terebratula biplicata* var. *dutempleana.* This probably represents an undescribed species of *Rectithyris.* They also referred some 'giant' terebratulids from the Shenley Limestone to *T. biplicata* Sowerby as the variety *gigantea.* The external and internal structures of these specimens suggest that they are in fact unusually large gerontic individuals of the Shenley species of *Rectithyris.*

The material studied is from the collections of the British Museum (Natural History) (BM) supplemented by the authors' own collecting. The collections at the Sedgwick Museum, Cambridge (SM), and the Institute of Geological Sciences, London (GSM), were also consulted, and material was obtained from the Natural History Museum in Brussels.

The techniques of serial grinding with a Croft grinder, supplemented by some dissection with mounted needles and a dental drill, were used to study the internal structures of the brachiopods. The serially ground surfaces of specimens were recorded on acetate peels which were then drawn and photographed with the aid of a Shadomaster projection apparatus. The internal structure of the brachiopods is represented by drawings of transverse serial sections, which usually represent only the brachial valve so that more details of hinge plate structure can be shown. All measurements given in the systematic descriptions are in millimetres (mm).

STRATIGRAPHICAL AND PALAEOECOLOGICAL BACKGROUND

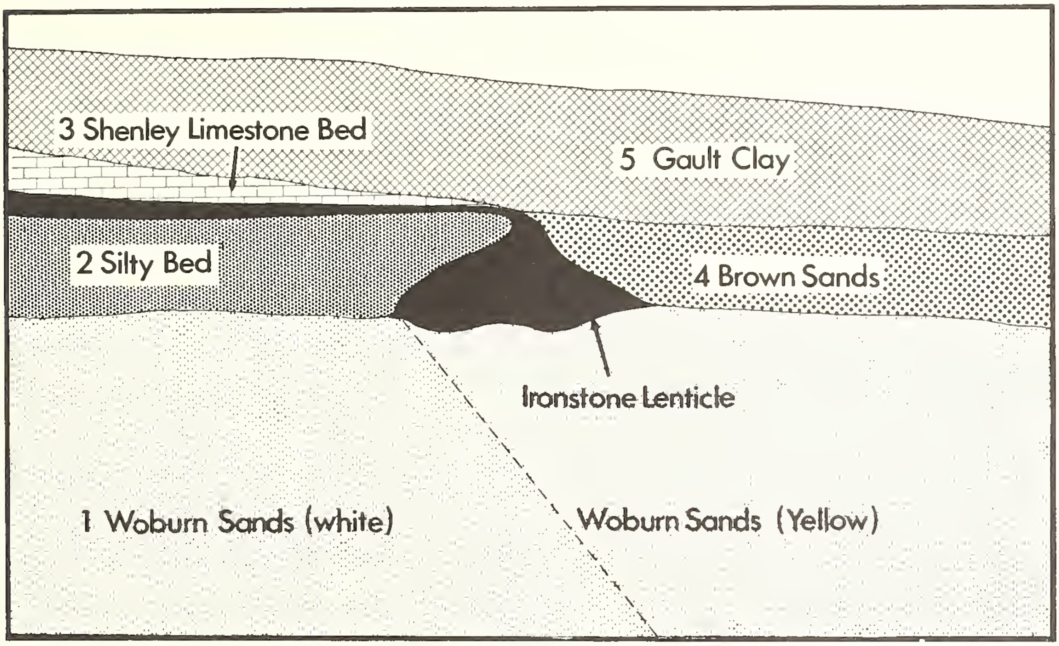
The Shenley Limestone occurs as part of a condensed bed of variable thickness, which lies at the base of the Gault, within the *regularis* Subzone of the *Leymeriella tardefurcata* Zone of the Lower Albian (Wright and Wright 1947). The bed is developed only in the region of Shenley Hill, approximately two miles (1·25 km) NW. of Leighton Buzzard, Bedfordshire. In this area the Woburn Sands (Aptian, at least in part) (Bed 1, text-fig. 1) are exploited for glass sands, and there are numerous pits which expose the base of the Gault. In the past the Shenley Limestone was more exposed than at present, and Lamplugh and Walker (1903) and Lamplugh (1922) described the exposures in some detail. Between 1963 and 1966 the limestone was exposed only in Mundays Hill pit (grid. ref. SP 940279) from which Cox made most of her observations and collections.

The stratigraphical relationship between the Shenley Limestone and other English Albian beds, especially its relationship with the nodule beds at the base of the Gault SE. of Shenley Hill, has been extensively investigated by several authors including Lamplugh and Walker (1903), Kitchin and Pringle (1920), Lamplugh (1922), Wright and Wright (1947), Casey (1961), and Bristow and Kirkaldy (1962). It is unnecessary here to enter into the stratigraphical argument and speculation that arose after the first description of these beds, but a brief description of the sediments of the Shenley Limestone bed and the mode of occurrence of the brachiopods therein may prove useful.

The bed (Bed 3, text-fig. 1) is composed mainly of iron-rich glauconitic sandstone in which the Shenley Limestone occurs as lenses and streaks of fine-grained, buff, or pink limestone and marl. At the base is a band of iron grit which rests non-conformably on laminated 'worm'-churned white sand and black clay (Bed 2, text-fig. 1, maximum thickness 4·5 m) which is unfossiliferous, although carbonaceous material is abundant. Lamplugh (1922) named this the 'Silty Bed' and interpreted it as representing estuarine conditions of deposition.

The top of the Shenley Limestone bed is brecciated, with a discontinuous development of secondary iron. A patchily developed band of red cirripede clay (Toombs 1935; Bristow and Kirkaldy 1962) overlies the limestone bed and passes up without a break, through a few centimetres of mottled green clays, into the overlying grey Lower Gault clays (Bed 5, text-fig. 1).

The Shenley Limestone is irregularly distributed throughout the sandstone bed (3) and is full of pebbles and grains of ironstone, quartz, and glauconite, all of which occur also as clastic components of the sandstone. The composition of the limestone approaches that of the sandstone as the percentage of clastic material increases. However, the junctions between sandstones and limestones are often sharp and marked by ribbons of ironstone which, by X-ray powder analysis, is shown to be probably goethite.



TEXT-FIG. 1. Diagrammatic section to illustrate the stratigraphical position of the Shenley Limestone bed at Leighton Buzzard.

Most of the limestone is hard but parts are in the form of soft marl which is identical in appearance and composition to the harder rock. Lamplugh (1922) mentioned soft, marly material but interpreted it as recently weathered limestone in which the fossil shells were fragile and decomposed. The soft marl found during the course of this work has usually come from a position deep within a mass of newly excavated rock and is unlikely to have been subject to weathering. The brachiopod shells from this marl are well preserved and show a wide size range. It is easier to extract the smaller, more fragile shells from this soft material than from the hard limestone but they are probably of no more frequent occurrence in the former than in the latter. Part of the harder limestone contains abundant, randomly orientated burrows, which indicate that it was once a soft, churnable mud. It is likely that the whole of the limestone was formed as a soft marl which has become differentially cemented leaving patches of the original unaltered material.

A purplish grey calcareous mudstone, composed largely of clay minerals, occurs in small lenses, interbedded with the cream coloured limestone and the sandstone. It is sparsely fossiliferous and has yielded specimens of the belemnite *Neohibolites minimus* but no brachiopods.

Throughout the Shenley Limestone small scale channels, load structures, and erosion surfaces are evident. Periods of deposition of coarse sand alternated with the deposition of calcareous mud. Periods of time when large quantities of coarse clastic material entered the area alternated with quieter periods when sedimentation and current activity were probably slacker. Frequent periods of erosion probably separated periods of sedimentation.

It is difficult to envisage the conditions under which the calcareous mud could have been deposited. Packed with a large variety of fossils, brachiopods being the most numerous, it is in direct contrast to the sandstone which contains only an occasional poorly preserved shell. During deposition the currents must have been strong enough to bring quite coarse clastic material into the area and would have been too strong to prevent the fine mud from settling. Lamplugh believed that shelly patches on the sea floor consolidated quickly and remained cemented there as limestone lenticles, while the loose sand was winnowed away from around them. Certainly the present lenticular form of the limestone shows that it must have been eroded at intervals, but the continued existence of the soft marl which has never been cemented, shows that Lamplugh's theory does not entirely explain the formation or preservation of the limestone. The fine-grained porcellanous texture of some of the limestone gives it a similar appearance to that of some calcite mudstones of algal origin and, although there are none of the laminar structures usually associated with limestones of this type, this kind of sediment is likely to be of algal origin. Possibly vegetation could have played a part in trapping sediment and slowing currents, but as yet no evidence for its former existence has been found.

The brachiopods apparently thrived while the limestone was being deposited, or during quiet periods of inhibited sedimentation. Their excellent state of preservation is probably the result of being engulfed and protected by the soft plastic mud soon after death. If any of the shells were deposited in the coarse sand they were probably destroyed quickly by abrasion and solution.

The following observations on the mode of occurrence of the brachiopods suggest that they form a life assemblage which is not quite in the position of life, e.g. it has been moved and re-sorted within the area in which the animals lived:

1. The brachiopod shells are always randomly orientated within the limestone.
2. Most of the shells are entire.
3. The state of preservation of the shells is usually excellent; fine ornament, e.g. the capilliform ornament of *Platythyris diversa*, is usually undamaged.
4. There is no marked separation of different sizes or shapes of shell, species, or age groups. Several species may be mixed together in close proximity, and little evidence has been found for the concentration of particular species in individual limestone lenticles as stated by Lamplugh and Walker (1903). There are no nests of one species

comparable with the nests of *Sellithyris sella* in the Aptian of the Isle of Wight (Middlemiss 1962). Sometimes several individuals of one species may be found in close proximity, suggesting that they may have been part of a nest which was broken up after death. Gerontic individuals and juveniles of the same species are often found together in the same block. Young immature shells are common in the limestone, and juvenile shells of only 3 mm length can be separated from the softer marl. The stiff plastic clay probably saved these very small shells from being winnowed away by the currents.

5. Each species of brachiopod shows a wide range of variation in external morphology, which probably indicates a wide range of minor variation in habitat developed within the area at the time. In addition to the wide range in variation in normal external features, abnormal deformation of the shell is unusually common. Large deformities of shape are probably due to development in crowded conditions, but small bumps at the shell margin were probably formed as a result of reaction to attack by parasites. In the present study serial grinding of a specimen of *Rectithyris shenleyensis* revealed a boring in the wall of the pedicle valve close to the beak. A hole must have been bored through the shell wall by a parasite and an obstruction left inside the shell adjacent to the hole. The innermost layer of the shell wall was then laid down with a bulge, so that a small chamber was formed over the inner end of the bored hole. This is an example of a deformity formed on the inside of the shell wall but deformities of the external shell wall are probably more common.

TERMINOLOGY

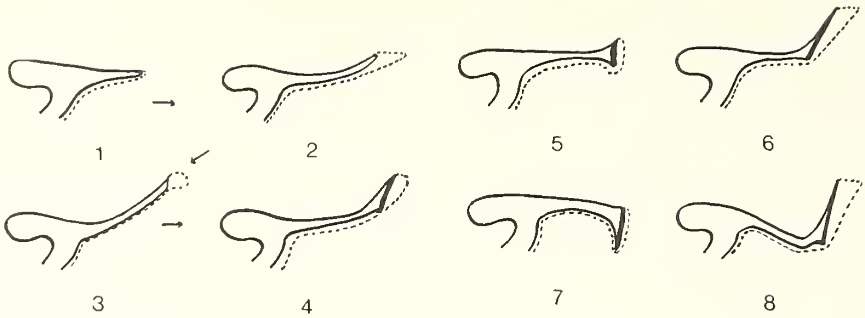
The terminology used in this paper follows the *Treatise on Invertebrate Paleontology, part H*, *Brachiopoda* (1965), and Middlemiss (1959). Certain terms, applying mainly to the hinge plates, are new or have been modified and are defined below.

Hinge plates

The hinge plates of the species investigated have a two-part structure. Each is composed of a 'primary' plate partially enclosed by a 'secondary' plate. The hinge plates are composed entirely of secondary layer material equivalent to the secondary layers of the shell wall (Williams 1956), and the terms used for the structure of the hinge plates are not equivalent to the terms 'primary' and 'secondary' as applied to the layers of the shell wall. Differences in the orientation of the calcite fibres of which they are composed probably enable the primary hinge plate to be distinguished from the secondary hinge plate in transverse section.

When the two part structure of hinge plates is taken into consideration, their classification involves the study of three important features (1–3 below) and terms describing variation in these features may be defined. The hinge plates of any species may be defined using a combination of these terms (text-fig. 2). Some of the terms used below are modified versions of terms introduced by Middlemiss (1959) and used in the *Treatise.*

1. *The width and concavity or convexity of the hinge plates.* In the living animal this was probably related to the size and shape of the attachment area of the dorsal adjustor muscle bases.



TEXT-FIG. 2. Explanation of terminology used to describe the structure of hinge plates in the Terebratulacea. Single hinge plates and inner socket ridges are shown in transverse section. The solid line represents the primary hinge plate and inner socket ridge; the broken line indicates the secondary hinge plate; the posterior extension of the crural base is shown in heavy black. 1, horizontal tapering; 2, concave, rounded, corniced; 3, concave, between rounded and cuneate, piped; 4, concave, cuneate, clubbed; 5, horizontal, cuneate, keeled; 6, horizontal, cuneate, clubbed; 7, convex, cuneate, keeled; 8, virgate, cuneate, clubbed.

Horizontal hinge plate. Not curved but flat; may be parallel to the commissural plane, or directed towards the floor of the brachial valve. Outline not greatly modified by secondary hinge plate development.

Concave hinge plate. Curved transversely, concave towards the pedicle valve. The curvature may be deep or shallow, and symmetrical or asymmetrical in transverse section.

Convex hinge plate. Curved transversely, convex towards the pedicle valve.

Virgate hinge plate. V-shaped in cross-section, concave towards the pedicle valve. This is an extreme case of a concave hinge plate.

2. *The form of the inner margin of the primary hinge plates.*

Tapering hinge plate. Tapers to a sharp edge running along its inner margin. The outline of this type of hinge plate is not usually modified by the secondary hinge plate which may be weakly developed.

Cuneate hinge plate. Thickens suddenly at its inner edge and ends abruptly with a flattened inner margin. The thick ends of the wedges of each pair of hinge plates are directed towards each other, while the thin ends pass outwards into the remainder of the hinge plates. The cuneate outline may be modified by the increased development of the secondary hinge plate. There are many variations of this type, involving changes in the proportion of the cuneate inner margin, but the construction remains basically the same. The increased downward extension of the cuneate inner margin produces a *keel.* The crural base usually extends posteriorly along the inner margin of a cuneate hinge plate between the primary and secondary portions of the hinge plate; its dorsal surface often enhances the keel.

In the living animal the cuneate type of hinge plate was probably associated with the need to provide a stronger 'anchorage' for the loop, and thus providing a greater support for the lophophore.

Rounded hinge plate. Has an inner margin which is gently rounded, i.e. it neither tapers to a sharp edge, nor is obviously cuneate.

3. *The degree of development of the secondary hinge plate.* This is always more strongly developed around the dorsal surface and inner edge of the hinge plate, away from the site of attachment of the dorsal adjustor bases. This development greatly modifies the outline of the hinge plates in transverse section. This is a source of possible confusion in the classification of the Terebratulacea, since much work has been based on the use of the *outline* of the hinge plates in transverse section as an important taxonomic character.

Clubbed hinge plate. The secondary hinge plate causes the outline to become thicker inwards, so that the inner margin is blunt or rounded. This is usually a modification of a cuneate primary hinge plate.

Piped hinge plate. A modification of a rounded or slightly cuneate hinge plate which becomes thinner inwards, but the inner margin is finished with a rounded thickened rim formed by the secondary hinge plate.

Corniced hinge plate. A modification of the rounded primary hinge plate in which the secondary hinge plate flares out into a cornice along the inner margin. Basically similar to the piped hinge plate.

The Terebratulacea appear to show a morphological progression from the tapering primary hinge plate, through the rounded to the cuneate form (text-fig. 2). In many species, e.g. *Rectithyris shenleyensis* (Walker) a progression from the rounded hinge plates in the extreme posterior umbo to the typical cuneate form developed anteriorly suggests that this morphological progression reflects a phylogenetic sequence which could have been repeated several times during the evolution of the Terebratulacea. Different species of the Terebratulacea, together possessing all types of hinge plate can be found in one bed of rock, e.g. the Shenley Limestone, showing that all types of hinge plates development occurred together at the same place and at the same point in geological time. The complete range of development of hinge plates of Terebratulacea since the early Mesozoic has not yet been worked out, but it seems that the form of the primary hinge plate may be of a considerable importance for the classification of the superfamily when used in conjunction with other morphological characters.

Ornament

The term 'ornament' is preferred to 'external sculpture'. 'Capillate ornament' is an ornament of capillae (fine radiating ribs more than 25 per 10 mm (Muir-Wood 1965) which are wavy and irregularly thickened along their lengths). It is characteristic of *Platythyris capillata* (d'Archiac).

GENERAL MORPHOLOGY OF THE SHENLEY LIMESTONE TEREBRATULACEA

All described species are biconvex when adult. The ventral profile varies, even within species, but transverse shells are rare. Depressed, compressed, and obese shells are all common, and younger individuals of a species may have depressed shells while the fully mature individuals of the same species may be compressed or obese. Very large size may be attained by fully mature or gerontic individuals of some species, e.g. *R. shenleyensis* (Walker). The beak angle varies between straight and incurved, although straight or incurved beaks are rare. Foramina may be telate, attrite, marginate, or labiate. They are usually mesothyrid, but may be permesothyrid. The foramen is usually large, but in a few individuals of all species it is tiny. The angle of truncation of the beak has a wide range of variation in most species. Variation in the beak angle produces a relative increase in the variation of the angle of truncation. The deltidial plates form a symphytium. In some species, e.g. *P. diversa* sp. nov. the apparent development of two separate deltidial plates is probably caused by a crack through the weakest point of the narrow-waisted symphytium. The anterior commisure is usually rectimarginate in juveniles and becomes uniplicate, sulciplicate, or episulcate. During ontogeny the sulciplicate stage may be derived from the rectimarginate stage without intervention of a uniplicate stage; this accords with the observations of Muir-Wood (1934) and Middlemiss (1959). Quadriplication and reversed plication are not found. Plication of the anterior commissure is not always accompanied by folding of the valves. When folding occurs it shows a wide range of development. In some species, e.g. *Boubeithyris boubei*, the brachial valve may be folded in reflection of the plication of the anterior commissure, while the pedicle valve remains unfolded.

The outer surface of the shells of most species is smooth. The species of *Platythyris* described here are exceptional in always having capillate ornament. Most species of Cretaceous terebratulids have fine striae visible in the inner layers of the shell wall.

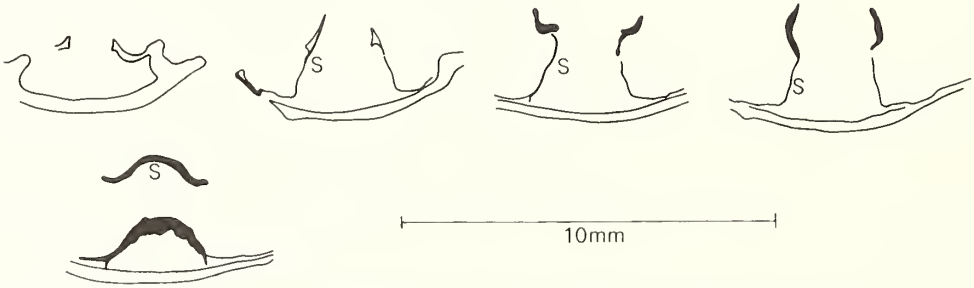
Examination of the microstructure of the shell wall shows that the primary layer (Williams 1956, 1966) is rarely visible in the Shenley Limestone Terebratulacea. The secondary fibrous and prismatic layers are well developed. In transverse section the fibres of the secondary layer show a saddle-and-keel structure similar to that described by Williams (1966) from recent Terebratulida.

Prismatic layers are well developed, especially in *B. boubei*, *R. shenleyensis*, and *P. diversa*, and show maximum development in the posterior part of each valve towards the mid line, i.e. in the older parts of the shell. In the extreme posterior of each valve there are often several thin prismatic layers alternating with fibrous layers. These thin layers merge antero-laterally into one thick prismatic layer which lies to the inside of a fibrous layer, and thins away at the anterior and sides of the shell. The prismatic layers are often more sharply defined on their inner surfaces; the outer surfaces often show a less sharp transition from the fibrous layer to the prismatic layer. The prismatic secondary layer is not developed in the hinge plates and hinge teeth but is well developed in the parts of the shell formerly occupied by the muscle bases. Its development does not appear to be associated with growth lines. The development of secondary prismatic layers varies in the shells of different species and probably in shells from different localities.

The descending branches of the loop diverge to varying degree e.g. × 4 in *B. boubei* and × 5 in *P. diversa*. The descending branches are recurved into the high or low arched transverse band.

The inner socket ridges vary in width and thickness in different species. The teeth are fairly massive in some species but may be thin and blade-like in others. The angle of insertion of the teeth and the height of the hinge plates above the floor of the brachial valve vary with the external proportions of the shell. Compressed, more obese, shells have a higher angle of insertion of the teeth, and the hinge plates are raised higher above the floor of the brachial valve. Wider, more depressed shells have a lower angle of insertion of the teeth and the hinge plates are closer to the floor of the brachial valve.

During the course of this work, several specimens of different species have been found to have a thin sheet of calcite extending from the lower edge of the loop to the floor of the brachial valve (see text-fig. 3 and Pl. 41, fig. 7). The term '*sub-loop skirt*' is proposed for this structure, which is attached to the loop but is



TEXT-FIG. 3. Transverse sections through a young specimen of *Rectithyris shenleyensis* sp. nov., Shenley Limestone, Leighton Buzzard, to show a sub-loop skirt(s).

separated from the floor of the brachial valve by a low gap that connects the anterior and posterior cavities of that valve. This structure may represent the posterior body wall of the living animal which has become calcified during life. It may have developed as a result of a 'physiological accident', or it may have had a strengthening or protective function. The sub-loop skirt does not have a spicular structure but has a somewhat similar position in the shell to the spicule skeleton described by Steinich (1963) in a *Terebratulina* from the Chalk of Rügen in the Baltic. The sub-loop skirt has been found by dissection of two specimens of *P. diversa* from the Shenley Limestone and has also been seen in transverse sections of *R. shenleyensis* (Walker), *P. diversa rubicunda* subsp. nov., and a specimen of *Moutonithyris moutoniana* (d'Orbigny) from France.

SYSTEMATIC DESCRIPTIONS

Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily SELLITHYRIDINAE Muir-Wood, 1965
Genus BOUBEITHYRIS gen. nov.

Type species. Terebratula boubei d'Archaic, 1847.

Diagnosis. Ventral profile pentagonal or pentagonal-oval. Valves equiconvex. Beak fairly wide, short or moderately short, sub-erect. Foramen mesothyrid; attrite or marginate. Angle of truncation of beak 90–100°. Anterior commissure rectimarginate to sulciplicate to episulcate. Folding usually confined to anterior third of the shell.

Hinge plates thin, concave, rounded, usually corniced. Inner socket ridges narrow. Crural processes high, fairly straight, tips inwardly inclined. Transverse band fairly high arched.

Range. Albian to Cenomanian.

Remarks. The name of the genus is derived from the name of the type species. It has been described only from the Shenley Limestone and the Cenomanian 'Tourtias' of Belgium.

Boubeithyris is assigned to the Sellithyridinae because of its thin, concave hinge plates with very small crural bases, the three septum-like ridges in the floor of its brachial valve, the thin descending lamellae and high-arched transverse band. It differs from other genera of this subfamily mainly in having corniced hinge plates. It is distinguished externally by the regular oval shape, narrowing anteriorly.

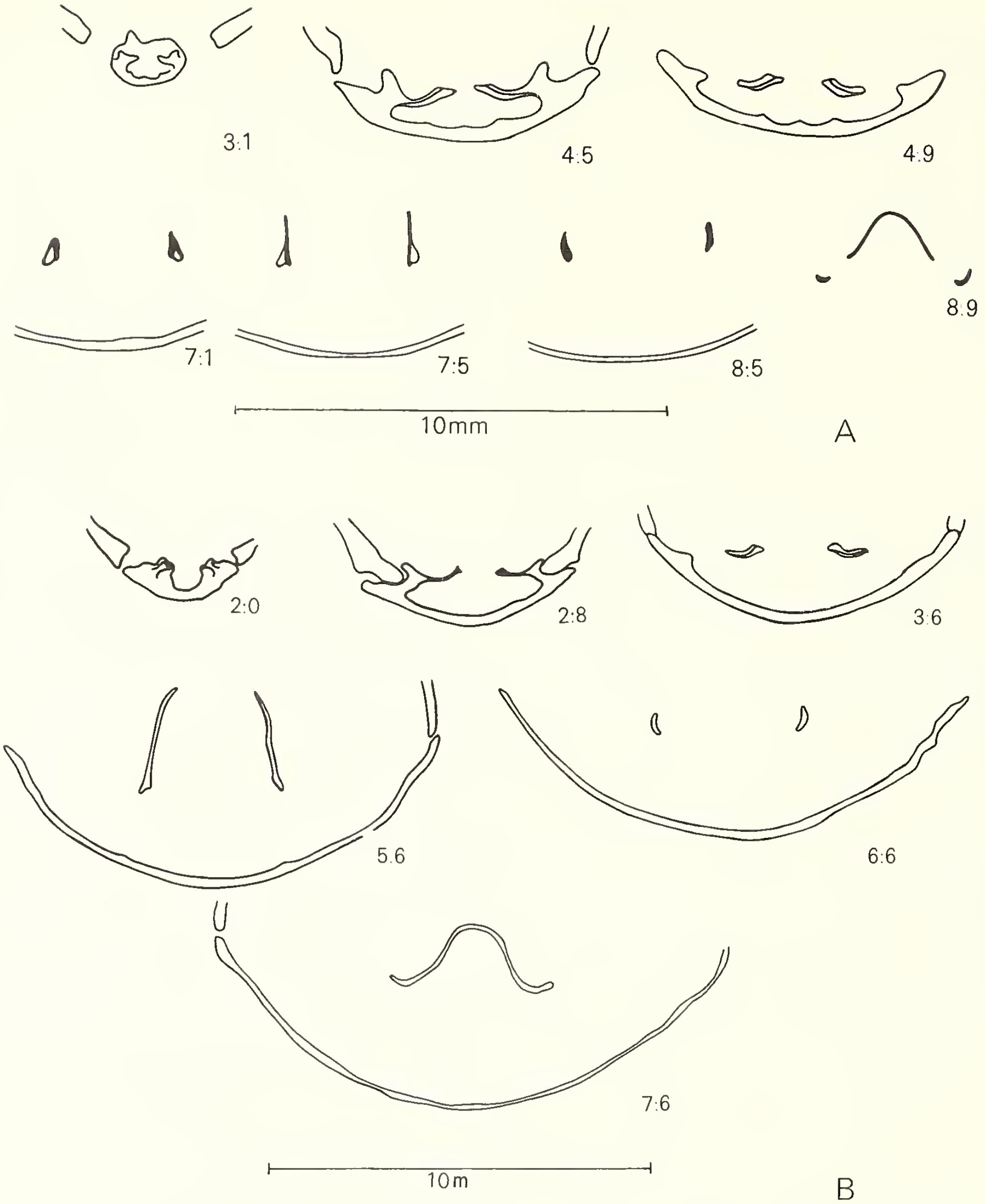
Species assigned. Boubeithyris boubei (d'Archiac); *B. buzzardensis* sp. nov.

Boubeithyris boubei (d'Archiac)

Plate 40, figs. 1–4; text-fig. 4

1847 *Terebratula boubei* d'Archiac, p. 320, pl. 19, fig. 11.
1903 *Terebratula boubei* d'Archiac; Lamplugh and Walker, p. 252, pl. 18, fig. 5.

Diagnosis. Boubeithyris of pentagonal oval ventral profile. P/A ratio 1 or slightly greater (rarely less than 1). Cardinal slopes straight. Beak sub-erect; beak ridges well defined, especially near the foramen which is large, circular, sometimes slightly telate or attrite, more commonly marginate. Anterior commissure rectimarginate to sulciplicate, rarely episulcate. Plication reflected by small folds and sulci at anterior end of brachial valve. Internal characters as diagnosed for the genus.



TEXT-FIG. 4. Transverse sections through two specimens of *Boubeithyris boubei* (d'Archiac). The concave, rounded, corniced hinge plates are seen in *a* at 4·5. The crural bases are attached to the extreme anterior ends of the hinge plates in *b* at 2·8. The high-arched transverse band is seen in *a* at 8·9 and in *b* at 7·6. *a*, BM BB76247, Shenley Limestone, Leighton Buzzard; *b*, BM BB76248, Tourtia (Cenomanian), Tournai.

Description. The ventral profile is usually pentagonal oval but some individuals, especially from the Shenley Limestone, may be more oval. More often, the anterior margin of the shell, although folded, has a 'squared off' appearance which enhances the pentagonal-oval outline.

Anterior commissure typically sulciplicate, but in a strongly folded shell may be slightly episulcate. At the other extreme some mature individuals are barely sulciplicate, retaining into maturity the rectimarginate condition of youth. No uniplicate individuals of this species have yet been found, and development appears to be straight from rectimarginate to sulciplicate. The plicae are close set and narrow, as are the folds at the anterior of the brachial valve, which are usually confined to the anterior third of the valve, or less. In extreme cases the folds may extend up to half the length of the valve. The pedicle valve may be gently folded at the tip or may show no folds at all. The shell usually shows no ornament, although fine radiating striae may be visible in the inner layers of some specimens.

The form of the hinge plates is fairly constant, but the corniced inner margins may be turned inwards from the vertical position so that in superficial appearance they approach the cuneate condition. Serial sections of one specimen showed short crural processes instead of the usual long pointed ones. It is possible that the long ends had been broken after death.

Neotype. The original specimens used by d'Archiac (1847) in his description of the species have been lost (Owen 1970, p. 55; confirmed by A. Dhont *in litt.*). A neotype resembling the specimen figured by d'Archiac 1847, pl. 20, fig. 1 is here chosen from the collections of the Institut Royal des Sciences Naturelles de Belgique in Brussels; registered number M.T.C. 10154 from the Tourtia of Tournai. Dimensions: length 31·0, width 17·0, thickness 12·0.

Remarks. In his original description d'Archiac (1847) described an ornament of radial lines on the outside of the shell. No true ornament has been observed during this work and d'Archiac was probably referring to the deep seated striae mentioned above.

Schloenbach (1867) believed '*T.*' *boubei* to be synonymous with '*T.*' *robertoni* d'Archiac, but his figure of a specimen of the latter from the Cenomanian Greensands of Quedlinburg (Harz) is rectimarginate and different in external form from the former. Some specimens of '*T.*' *robertoni* from the Tourtia of Tournai resemble some *B. boubei* in profile and beak characters, but the typical folding is absent. A specimen of *T. robertoni* from Tournai was sectioned and showed that the internal characters, especially the hinge plates, are fairly similar to those of *B. boubei*. The hinge plates of *T. robertoni* are concave with rounded inner margins but there are no secondary cornices as in *B. boubei*. The hinge plates of *T. ovata* Sowerby from the Warminster Greensand are similar to those of *T. robertoni* and all of these species may be related.

Meyer (1864) identified some single valves from the Lower Greensand pebble bed (Upper Aptian) of Godalming, Surrey, as this species. Davidson (1874) figured, after Meyer, a specimen as *T. boubei* from Godalming. This figure shows two deltidial plates, an anterior commissure which is slightly uniplicate, and a beak which is too long for *B. boubei*. The original specimen figured by Meyer is in the Sedgwick Museum in Cambridge and is a terebratellidine. Lamplugh and Walker (1903) figured specimens which they collected from the Shenley Limestone and recognized that they belonged to the d'Archiac species *T. boubei*.

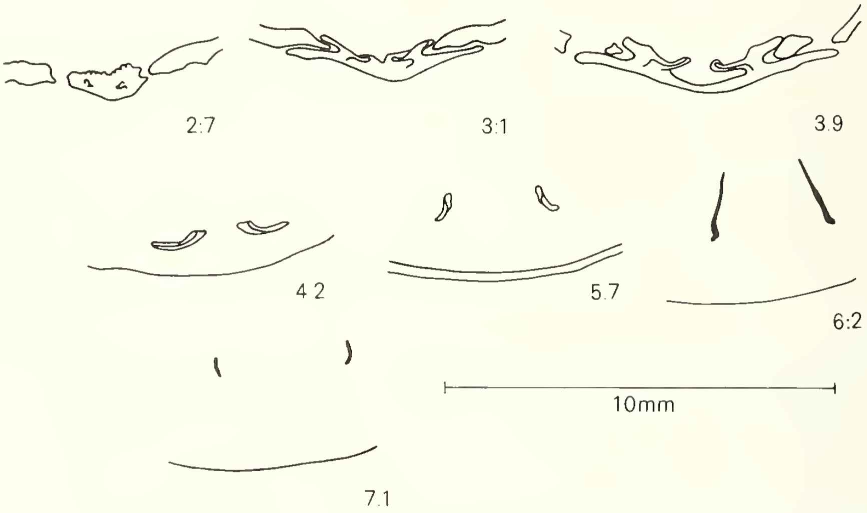
Although there may be some slight differences between some Shenley individuals of this species and some from the Tourtias, many individuals are identical. The hinge plates of some Tourtia individuals are thinner but present knowledge does not justify separation of Albian and Cenomanian members of this species.

Boubeithyris buzzardensis sp. nov.

Plate 40, figs. 5, 6; text-fig. 5

1903 *Terebratula ovata* Sowerby; Lamplugh and Walker, p. 252, pl. 17, fig. 6.

Diagnosis. Boubeithyris of pentagonal or pentagonal-oval ventral profile. P/A ratio 1–0·6. Foramen large, circular, attrite. Symphytium wide but short, well exposed. Beak ridges well defined. Cardinal slopes straight or slightly concave. Development of anterior commissure rectimarginate to sulciplicate to episulcate. Plication reflected by strong folds and sulci in anterior third of both valves. Internal structure as diagnosed for the genus.



TEXT-FIG. 5. Transverse sections through *Boubeithyris buzzardensis* sp. nov. The hinge plates within the cardinal process are markedly concave (2·7). At 3·9 and 4·2 the concave, rounded, corniced hinge plates are seen. BM BB76249, Shenley Limestone, Leighton Buzzard.

EXPLANATION OF PLATE 40

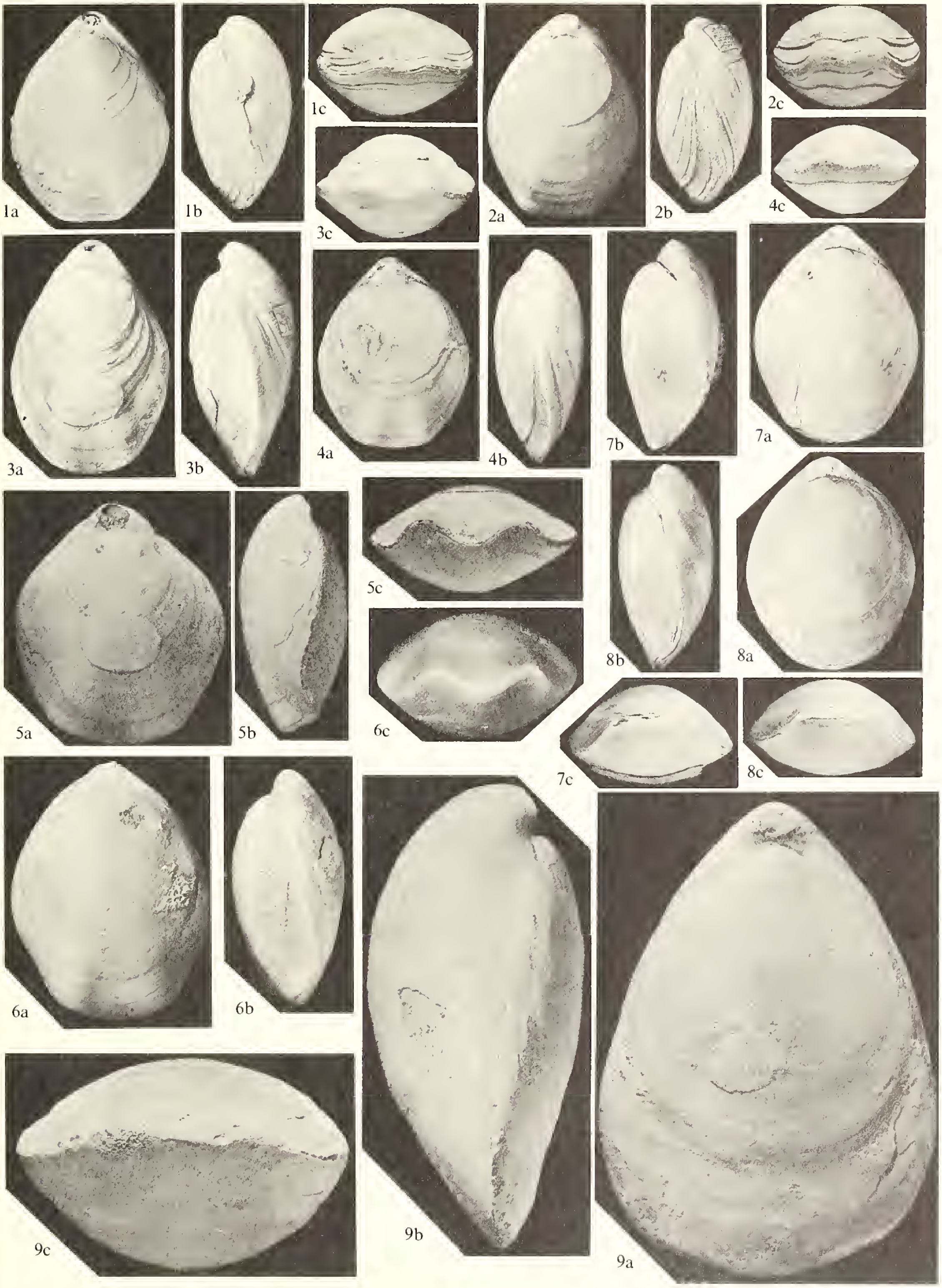
All figs. × 1·5.

Figs. 1–4. *Boubeithyris boubei* (d'Archiac). 1*a–c*, Neotype, M.T.C. 10154, Tourtia (Cenomanian), Tournai, Belgium. 2*a–c*, strongly biplicate specimen, BM BB76230, Tourtia, Tournai. 3*a–c*, pentagonal specimen, BM B26193, Shenley Limestone, Leighton Buzzard. 4*a–c*, an oval specimen, BM BB76231, Shenley Limestone.

Figs. 5, 6. *Boubeithyris buzzardensis* sp. nov., Shenley Limestone, Leighton Buzzard. 5*a–c*, BM B26199, Holotype. 6*a–c*, BM BB76233.

Figs. 7, 8. *Walkerithyris mendax* sp. nov., Shenley Limestone, Leighton Buzzard. 7*a–c*, BM BB76234, Holotype. 8*a–c*, a specimen with squarer uniplication, BM BB76235.

Fig. 9*a–c*. *Rectithyris shenleyensis* (Walker), Shenley Limestone, Leighton Buzzard. A typically triangular specimen, BM B26166.



COX and MIDDLEMISS, Cretaceous Terebratulacea

Description. The main characteristics of this species are the ventral profile, short beak, sulciplicate or episulcate anterior commissure, and well developed folds which affect the anterior of both valves equally. Variation depends on the differences in the ratio of length to width and small differences in the degree of folding. The shell is smooth except for some well-spaced growth lines that are quite prominent.

Holotype. BM B26199, from the Shenley Limestone. Figured on Pl. 40, fig. 5*a–c*. Dimensions: length 25·5, width 22·6, thickness 12·0.

Remarks. This species was identified by Walker (Lamplugh and Walker 1903) as *T. ovata* Sowerby, after he had compared specimens from the Shenley Limestone with *T. ovata* from the Warminster Greensand (Cenomanian). He believed that they did not differ any more than the species varied at Warminster. Re-examination of the materials shows that there are differences between the two species, although a few specimens of each tend to approach each other in external structure. The most important difference lies in the plication of the anterior commissure and the folding of the valves. The anterior commissure of *T. ovata* is sulcate or paraplicate, but that of *B. buzzardensis* is sulciplicate or episulcate. The long deep median sulcus on the brachial valve and the long median rib on the pedicle valve typical of *T. ovata* are absent from *B. buzzardensis*, which has evenly developed folds and sulci in the anterior third of each valve. The beak of *B. buzzardensis* is shorter, the P/A ratio lower, the valves more depressed, and the ventral profile more pentagonal. It has no ornament. The internal structure of these two species is similar but the secondary 'cornices' at the inner margins of the hinge plates are absent from *T. ovata*.

B. buzzardensis differs from *B. boubei* mainly in having a smaller beak, a lower P/A ratio, and folds which affect both valves equally. There is considerable difference in external form between extreme variations of one species and those of the other, but some less elongate and more pentagonal individuals of *B. boubei* closely resemble more oval, less strongly folded individuals of *B. buzzardensis*. However, the ratio of length to width of *B. buzzardensis* is usually lower and episulcate anterior commissures are more common.

Other species of English Albian Terebratulidae are distinct from *B. buzzardensis* in size, types of folding, beak characters, and internal structure. The species name is derived from the town of Leighton Buzzard in Bedfordshire.

Genus WALKERITHYRIS gen. nov.

Type species. Walkerithyris mendax sp. nov. (= *Terebratula moutoniana* d'Orbigny; Walker 1903).

Diagnosis. Ventral profile pentagonal. Brachial valve more obese than pedicle valve. Beak short, wide, suberect to nearly straight. Beak ridges fairly well defined, especially near the foramen. Symphytium short, wide. Foramen circular, mesothyrid; telate, attrite or slightly marginate, anterior commissure uniplicate. Hinge plates wide, thin, deeply concave, piped.

Known range. Albian.

Description. The lateral commissure is strongly convex towards the pedicle valve in the anterior part of the shell. The brachial valve is gently folded with a wide, median longitudinal fold that reflects the uniplicate anterior commissure and affects at least half the length of the valve. The pedicle valve is flattened and spatulate at the anterior end. The inner socket ridges are wide, with the upper surfaces convex towards the pedicle valve. None of the serial sections prepared so far has shown the loop, which is fragile and breaks easily.

Remarks. This genus is erected for the type species alone. It is distinguished from other English Albian genera by the form of the hinge plates and external features of the shell. The hinge plates are similar to those of the lower Cretaceous continental species *Loriolithyris russillensis* (de Loriol) and *Loriolithyris valdensis* (de Loriol). The wide piped hinge plates found in these species and described by Middlemiss (1968) are not commonly found in Cretaceous Terebratulidae and it might seem reasonable to include all species which possess them in the same genus. However, the external features of *Walkerithyris* are very different from those of the above mentioned species. *L. valdensis* and *L. russillensis* have massive beaks, strong plication and strongly folded valves. At present, without any more evidence to connect them, it is impossible to include these species and *W. mendax* in the same genus.

Walkerithyris mendax sp. nov.

Plate 40, figs. 7, 8; text-fig. 6

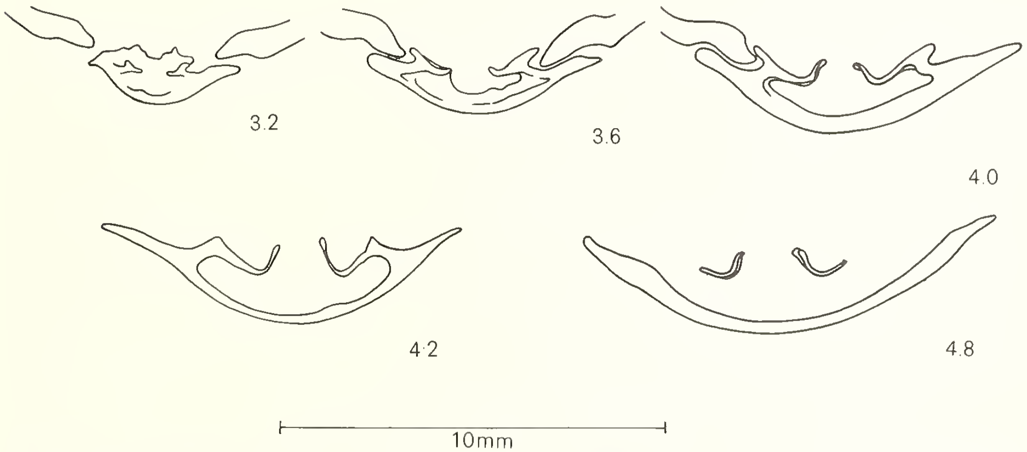
1903 *Terebratula moutoniana* d'Orbigny; Walker, p. 251, pl. 18, fig. 4*a*, *b* (non *Terebratula moutoniana* d'Orbigny 1849).

Diagnosis. External and internal structure as diagnosed for the genus. P/A ratio 1–0·5. Cardinal slopes straight or slightly convex. Angle of truncation of the beak about 90°.

Description. This species varies mainly in the ratio of width to length, the P/A ratio and the degree of uniplication of the anterior commissure. Some individuals are much longer than wide and have a more oval profile than others. The P/A ratio is normally about 1 but may be as low as 0·5. The uniplication may be very gentle or quite strong. Where the uniplication is strong the anterior end of the pedicle valve becomes increasingly flattened and spatulate.

Holotype. BM BB76234, from the Shenley Limestone. Dimensions: length 23·0, width 17·5, thickness 10·5.

Remarks. Walker (1903) identified this species as *Terebratula moutoniana* d'Orbigny. Other English specimens which Walker identified as *moutoniana* were from the Aptian



TEXT-FIG. 6. Transverse sections through *Walkerithyris mendax* sp. nov. The concave, piped hinge plates characteristically have a slightly sinuous outline, as at 4·0 and 4·8. BM BB76250, except for section 4·2, which is from BM BB76251; both from the Shenley Limestone, Leighton Buzzard.

of Brickhill and Upware, but these were later included by Middlemiss (1959) in a new genus, *Platythyris.*

Walkerithyris mendax differs from *Moutonithyris moutoniana* (d'Orbigny) primarily in its internal structure, but also differs externally. *M. moutoniana* as figured by d'Orbigny (1849) is more oval in shape, the ventral valve is more convex than the dorsal, the lateral commissure is straight for most of its length, the plication is more angular and the beak is longer and more erect. The typical adult *M. moutoniana* is much larger than *W. mendax*. The keeled, cuneate hinge plates of *M. moutoniana* (d'Orbigny) are in sharp contrast to the piped hinge plates of *W. mendax*. *W. mendax* resembles the Aptian species *Platythyris comptonensis* Middlemiss in its external features but the latter species is more oval, has a P/A ratio greater than 1, and has poorly defined beak ridges. The structure of the hinge plates of the two species is quite different; *P. comptonensis* has horizontal, tapering hinge plates while those of *W. mendax* are concave and piped. The form of the hinge plates and inner socket ridges distinguish this species from other English Albian species. The name of the species is derived from its deceptive external appearance which has caused it to be confused with other species in the past.

Subfamily RECTITHYRIDINAE Muir-Wood, 1965

Genus RECTITHYRIS Sahni, 1929

Type species. Terebratula depressa Lamarck, from the Cenomanian Tourtia, Belgium.

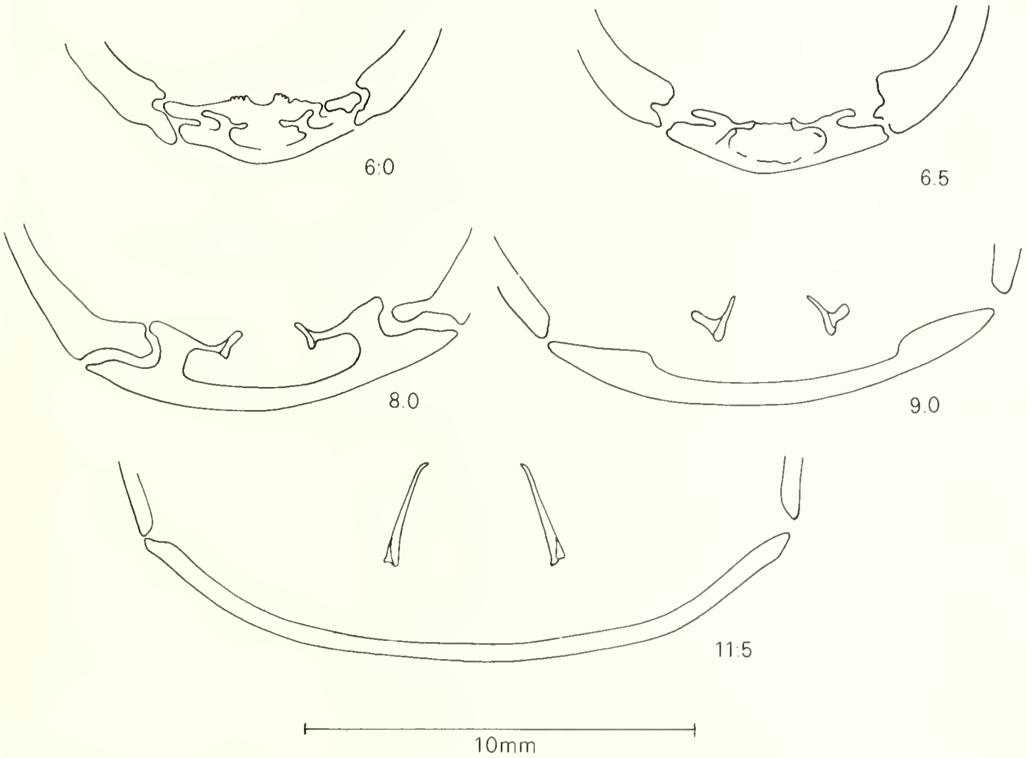
Emended diagnosis. Ventral profile variable. Beak straight to erect. Foramen telate, attrite, marginate, or sometimes labiate. Symphytium large, often well exposed. Anterior commissure rectimarginate to uniplicate, or rectimarginate to sulciplicate without uniplicate intermediate stage; fully mature adults with rectimarginate anterior commissures common. Shell smooth.

Cardinal process low, small, flat. Inner socket ridges narrow, fairly thick, upper surfaces convex. Hinge plates thin, wide, slightly concave to virgate; cuneate, may be keeled. Crural bases attached to the flat inner margins of the anterior ends of the hinge plates. Crural processes high, thin pointed; fairly straight but bases and tips often concave towards each other. Crural flanges and keels small or rudimentary. Descending branches of loop thin; transverse band high arched.

Range. Albian to Cenomanian.

Remarks. This genus was erected by Sahni (1929) for *T. depressa* Lamarck, and he also included several other species described by d'Archiac from the Tourtia of Belgium. In the past the type species has been described and discussed by many authors (Schloenbach 1867; Pictet 1872; Davidson 1852; Lamplugh and Walker 1903) and many Cretaceous species have been included in it. Middlemiss (1959) erected a new genus *Cyrtothyris* to include the English Aptian species formerly included in *T. depressa*. *Cyrtothyris* is closely related to *Rectithyris* and Middlemiss, in discussing the differences between the two genera, stated that 'the nature of the relationship is obscure in the present (1959) state of knowledge of the Albian terebratulids'. These Albian species which are described below and which were included in *T. depressa* Lamarck by Lamplugh and Walker (1903) thus hold an important position between the two genera.

In comparing the Albian species with those of the Aptian and Cenomanian, past authors have used different methods of recording their internal structures. The Albian species described here have been studied by the use of acetate peels to record the serially ground transverse sections of the shell. This method, which allowed more details of shell structure to be shown, has proved more successful than former methods. For example, the use of peels shows the structural relationships between different types of hinge plates which is of particular importance in the study of the phylogeny and classification of these Cretaceous genera. Middlemiss (1959) used the form of the hinge plates and crural processes to differentiate *Cyrtothyris* from *Rectithyris*. He described the hinge plates of *Cyrtothyris* as clubbed and virgate, with the inner lamina the same length as the outer in transverse section; crural flanges and keels were well developed. In the same publication Middlemiss described *Rectithyris* as having virgate hinge plates, with the inner lamina shorter than the outer in transverse section. The hinge plates were keeled, but there were no true crural flanges or crural keels. Acetate peels show that *R. depressa* has slightly concave, cuneate hinge plates, but otherwise the internal structure is much as described by Middlemiss. The crural bases are attached to the inner margins of the hinge plates, so accentuating the keel; crural flanges and crural keels are indeed rudimentary. The Albian species of *Rectithyris* described below have



TEXT-FIG. 7. Transverse sections through *Rectithyris depressa* (Lamarck). The hinge plates are initially horizontal, cuneate (6·0 and 6·5) and become cuneate, keeled (8·0). The crura are flanged and slightly keeled (9·0 and 11·5). BM duplicate specimen, Tourtia (Cenomanian), Tournai.

concave to slightly convex cuneate hinge plates which have crural bases attached to their anterior inner edges. The keels, if developed at all, are very rudimentary; small crural flanges and keels are frequently, but not always, developed. The extreme posterior ends of the hinge plates are sometimes covered with sufficient secondary material to appear 'clubbed'. The internal characteristics of the Albian species suggest that they should be included in the genus *Rectithyris* but that they probably represent an intermediate position between *Cyrtothyris* and *Rectithyris*.

In external features the Albian species often closely resemble the Aptian species. Slightly labiate foramina described by Middlemiss in *Cyrtothyris* are well developed in the Albian *R. shenleyensis*. Various degrees of inflation, compression and plication of the shell, which Middlemiss described as common in fully mature and gerontic individuals of *Cyrtothyris*, are also commonly found in *Rectithyris*.

The divided inner hinge plates described by Sahni (1929) as characteristic of this genus, have not been seen in any of the numerous Albian and Cenomanian specimens examined in this study.

In his original description Sahni included the d'Archiac species *T. robertoni*, *T. viquesneli*, *T. tornacensis*, *T. roemeri*, *T. bouei*, and *T. crassa* in this genus because of the characters of beak and foramen, quoting d'Archiac's figures and descriptions. '*R.*' *roemeri* and '*R.*' *bouei* have not been sectioned in the present study, but the small size and strongly biplicate external form suggests that they do not belong to this genus. *R. viquesneli* is probably a young stage of *R. depressa* (Davidson 1855; Middlemiss 1959). *R. tornacensis* was included by Middlemiss in *Sellithyris*. '*R.*' *robertoni* and '*R.*' *crassa* have been sectioned, and should be separated from *Rectithyris* by features of the cardinalia, especially the structure of the hinge plates which is similar to that found in *Boubeithyris* gen. nov.

Specimens from the Warminster Greensand (Cenomanian) in the collections of the Geneva Natural History Museum resemble *R. shenleyensis* in external form. The structure of the hinge plates of a similar specimen from the British Museum (Natural History) collection (B25239) which was sliced also suggests reference to *Rectithyris*.

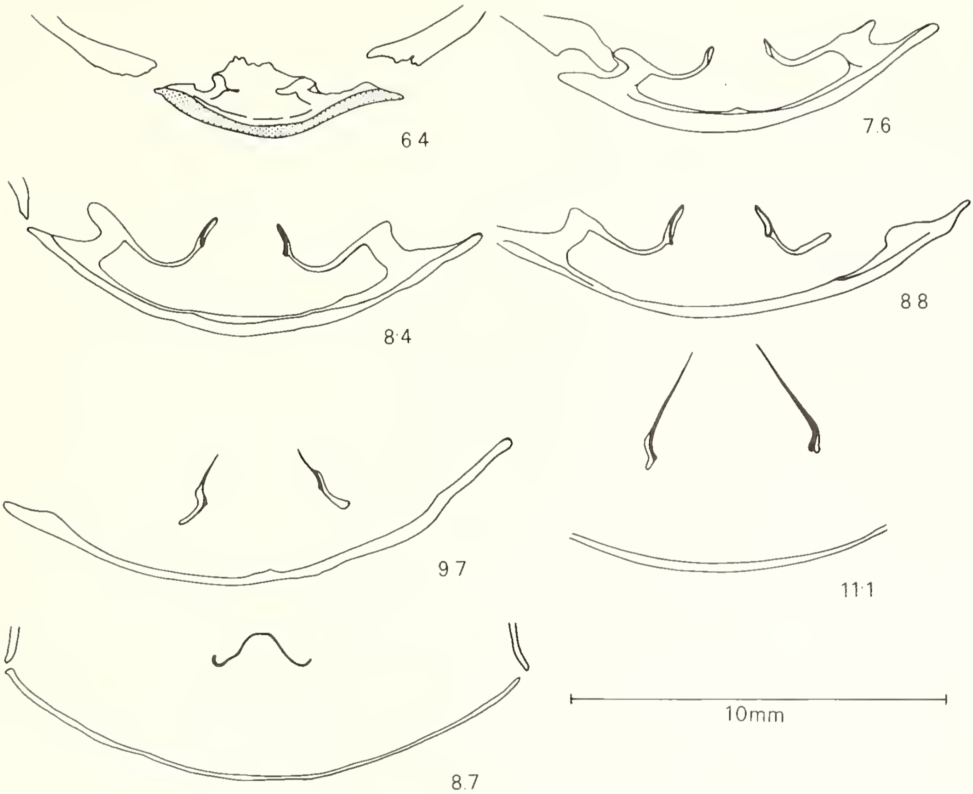
Species assigned. R. depressa (Lamarck); *R. shenleyensis* (Walker); *R. shenleyensis heathensis* subsp. nov.

Rectithyris shenleyensis (Walker)

Plate 40, fig. 9; Plate 41, figs. 1–4; text-fig. 8

1903 *Terebratula depressa* Lamarck var. *shenleyensis* Walker; Lamplugh and Walker, p. 251, pl. 17, figs. 1*a*, *b*.

Diagnosis. Triangular or oval ventral profile. P/A ratio 1 or commonly greater than 1. Cardinal slopes convex or straight. Pedicle valve slightly more convex than brachial valve. Shell depressed, especially in younger growth stages, inflated, and slightly compressed with age. Anterior commissure rectimarginate, becoming slightly sulciplicate in some fully mature adults without intervening uniplicate stage. Beak ridges well developed. Beak erect or suberect. Foramen mesothyrid, telate, attrite, marginate or slightly labiate. Hinge plates thin, wide, strongly concave, cuneate, may be slightly keeled. Crural bases attached to anterior inner margin of hinge plates. Crural processes high, pointed, inwardly inclined, fairly straight except for curved base. Small crural flange and keel usually present.



TEXT-FIG. 8. Transverse sections through *Rectithyris shenleyensis* (Walker). The hinge plates are initially horizontal (6·4), becoming concave, cuneate, keeled (7·6–8·8). BM B26236, except for section 8·7, which is from BM BB76252; both from the Shenley Limestone, Leighton Buzzard.

Description. The triangular ventral profile of the adult of this species is very characteristic. Adult individuals may be more oval when the P/A ratio approaches 1. Young individuals are depressed, have an oval ventral profile and an almost flat brachial valve, a rectimarginate anterior and an erect or suberect beak, often with a small circular foramen. In the adult, sulciplication of the anterior commissure may occur with or without increased inflation of the shell, but occurs only in fully mature or gerontic individuals. A slightly labiate foramen is common; the combination of such a foramen with the telate condition produces the characteristic 'keyhole' shape seen in many specimens.

Lectotype (here chosen). GSM 51262, figured by Lamplugh and Walker 1903, pl. 17, figs. 2*a*, *b*; from the Shenley Limestone.

Rectithyris shenleyensis heathensis subsp. nov.

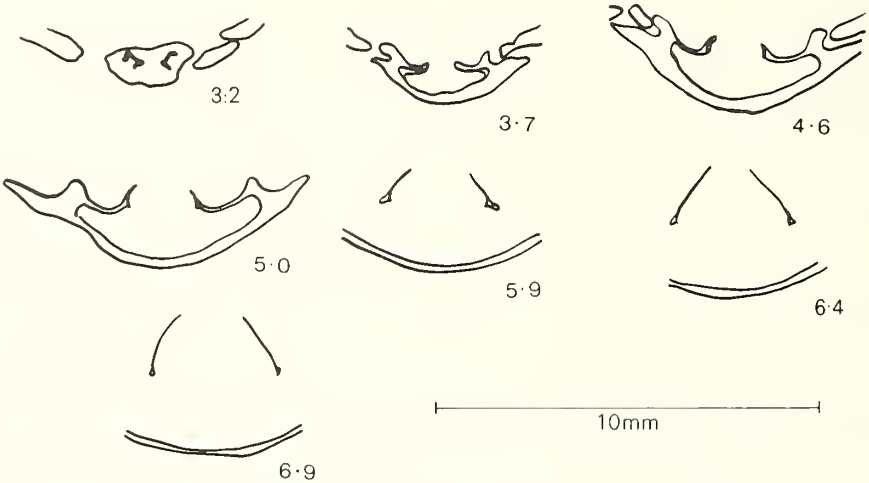
Plate 41, fig. 5; text-fig. 9

Diagnosis. R. shenleyensis of pentangular-oval or rhomboidal ventral profile, valves often equally convex. P/A ratio 1 or slightly more. Beak short, wide, sub-erect to nearly straight. Foramen mesothyrid, large, circular. Symphytium well exposed, beak ridges well defined. Anterior commissure gently uniplicate from an early age. Lateral commissure gently arched. Gentle fold in anterior half of brachial valve; anterior half of pedicle valve somewhat spatulate. Internal characters as for *R. shenleyensis.*

Description. The ventral profile, which is pentangular-oval to subcircular, with some individuals developing a pentagonal or rhomboidal outline, and the uniplication are the main distinguishing features of this subspecies.

Holotype. BM BB76241, from the Shenley Limestone. Dimensions: length 31·0, width 26·5, thickness 14·5.

Remarks. R. shenleyensis heathensis resembles *C. uniplicata* (Walker) from the English Aptian, but the beak ridges of the former are more distinct and the beak is usually wider and less conical. The P/A ratio of the Aptian species is greater and the pedicle valve has a slight sulcus in the anterior half. Uniplicate varieties of *R. depressa* from the Tourtias are larger, have longer, more produced beaks and may develop slight



TEXT-FIG. 9. Transverse sections through *Rectithyris shenleyensis heathensis* subsp. nov. The initially horizontal hinge plates are seen within the cardinal process at 3·2; they become concave, cuneate, and slightly keeled at 4·6 and 5·0. The crura are flanged and slightly keeled at 5·9–6·9. BM B26176, Shenley Limestone, Leighton Buzzard.

EXPLANATION OF PLATE 41

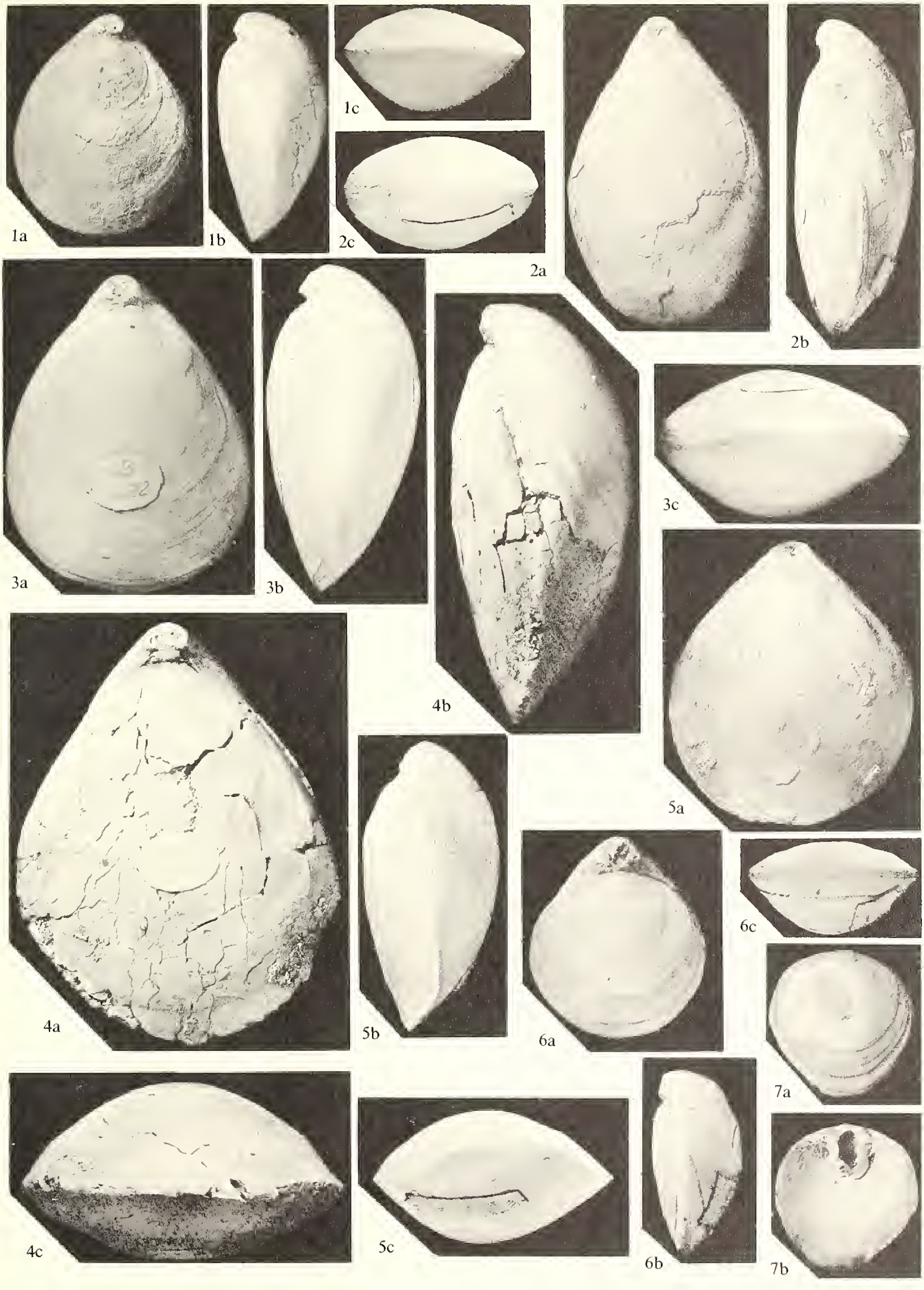
All figs. × 1·5.

Figs. 1–4. *Rectithyris shenleyensis* (Walker), Shenley Limestone, Leighton Buzzard. 1*a–c*, young, gently uniplicate specimen, BM BB76239. 2*a–c*, an elongate specimen, BM BB76240. 3*a–c*, a slightly biplicate specimen, BM BB76236. 4*a–c*, a gerontic specimen, BM BB76238.

Fig. 5*a–c*. *Rectithyris shenleyensis heathensis* subsp. nov., Shenley Limestone, Leighton Buzzard. Holotype, BM BB76241.

Fig. 6*a–c*. *Platythyris capillata* (d'Archiac), Tourtia (Cenomanian), Tournai, Belgium. A young, rectimarginate specimen, BM B35421.

Fig. 7*a*, *b*. *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. A brachial valve dissected to show the sub-loop skirt. The loop was broken during dissection and is incomplete above the anterior part of the skirt.



COX and MIDDLEMISS, Cretaceous Terebratulacea

sulciplication which is never developed in *R. shenleyensis heathensis*. The name of the subspecies is derived from the name of Heath and Reach, a village near Shenley Hill, Bedfordshire.

Family PYGOPIDAE Link, 1830
Subfamily PLATYTHYRIDINAE Dieni and Middlemiss, 1975
Genus PLATYTHYRIS Middlemiss, 1959

Type species. Platythyris comptonensis Middlemiss, 1959.

Diagnosis (after Dieni and Middlemiss, 1975). Shell elongate, oval or pear-shaped. Lateral commissure arched; anterior commissure rectimarginate, uniplicate, sulciplicate, or gently sulcate. Shell capillate, or smooth with more or less obvious longitudinal striae. Umbo suberect to erect. Foramen mesothyrid to permesothyrid. Symphytium short or very short. Beak ridges rounded. Cardinal process small. Hinge plates horizontal to very slightly concave, tapering, or with rounded inner margins; becoming cuneate and keeled in gerontic stage. Crural processes incurved. Loop short; transverse band low-arched.

Range. Upper Aptian to Cenomanian.

Remarks. The angle of truncation has a wide range, between 90° and 100°, in this genus. The anterior commissure is always rectimarginate in the young, but may be uniplicate to sulciplicate or sulcate in adults.

Species assigned. P. comptonensis Middlemiss, 1959; *P. minor* Middlemiss, 1959; *T. capillata* d'Archiac, 1847; *P. floresana* Dieni and Middlemiss, 1975; *P. diversa* sp. nov.

Platythyris capillata (d'Archiac)

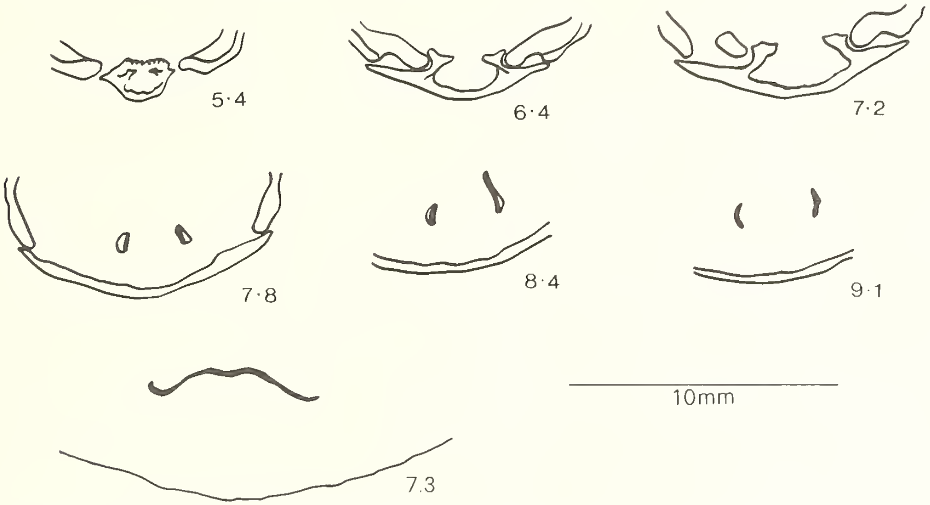
Plate 41, fig. 6; Plate 42, figs. 1, 2; text-fig. 10

1847 *Terebratula capillata* d'Archiac, pl. 20, figs. 1–3.
1867 *Terebratula capillata* d'Archiac; Schloenbach, p. 454.
1871 *Terebratula capillata* d'Archiac; Quenstedt, p. 385, pl. 17, figs. 75–76.
1972 *Platythyris capillata* (d'Archiac); Popiel-Barczyk, p. 142, pl. 2, fig. 8, pl. 4, fig. 1.
1974 *Capillithyris capillata* (d'Archiac); Katz, p. 258, pl. 84, fig. 12*a–c*.

Diagnosis. Ventral profile circular to oval. Valves equiconvex. P/A ratio 1 or less. Beak sub-erect, beak ridges well defined. Foramen large, circular, attrite or marginate, mesothyrid. Symphytium short but well exposed. Cardinal slopes straight or slightly concave. Anterior commissure rectimarginate to gently uniplicate to slightly sulciplicate, sometimes slightly sulcate. Hinge plates thick, narrow. Crural processes thick, low with blunt tips. Width of loop at transverse band twice its width at anterior ends of hinge plates.

Neotype. The original specimens used by d'Archiac (1847) are lost (Owen 1970, p. 55; confirmed by A. Dhont *in litt.*). A neotype resembling the specimen figured by d'Archiac 1847, pl. 20, fig. 1 has been chosen from the collections of the 'Institut Royal des Sciences Naturelles de Belgique' in Brussels, and is figured here on Pl. 42, fig. 1. Registered number M.T.C. 10156 from the Tourtia of Tournai. Dimensions: length 34·0, width 32·0, thickness 18·0.

Remarks. D'Archiac (1847) recognized different varieties of this species but did not indicate the considerable intermediate variation which occurs between his chosen varieties. Many specimens closely resemble d'Archiac pl. 20, fig. 1 and have circular ventral profiles, fairly small, somewhat produced beaks, large circular foramina, slightly concave cardinal slopes and rectimarginate or slightly sulciplicate anterior commissures. Specimens which resemble d'Archiac var. a, pl. 20, fig. 2 have oval, ventral profiles, are often obese, have slightly sulciplicate or sulcate anterior commissures, and fairly large wide beaks. The specimens resembling d'Archiac var. b, pl. 20, fig. 3, are smaller, fairly depressed and have rectimarginate anterior commissures; these are certainly juveniles of the other varieties.



TEXT-FIG. 10. Transverse sections through *Platythyris capillata* (d'Archiac). The horizontal, tapering hinge plates are seen at 5·4–7·2, the subrectangular free bases of the crura at 7·8, and the low-arched transverse band at 7·3. BM 3412, except for section 7·3, which is from BM 35422; both from Tourtia (Cenomanian), Tournai.

Three specimens from Tournai were sectioned to show the internal structure. One was a young specimen but the other two corresponded in external appearance to d'Archiac pl. 20, figs. 1, 2.

The young specimen and the d'Archiac var. a. were shown to have the horizontal, tapering hinge plates typical of the genus (text-fig. 10). The other specimen, similar to d'Archiac's fig. 1 in external appearance was found to have thick, horizontal hinge plates which did not taper, but the inner margins were deflected sharply downwards at right angles to the rest of the plate; the crural base was extended along the inner margin of the hinge plate for much of its length. This type of construction was not found in any other specimens of the species and appears to be a gerontic modification of the normal type of hinge plate structure; it occurs also in *P. diversa.* D'Archiac figured specimens with disjunct deltidial plates and this condition has been observed in many specimens examined by the authors, but has proved to be the result of fracturing through the narrow 'waist' of the symphytium.

Schloenbach (1867) mentioned that '*T.*' *capillata* occurred in the Cenomanian of Germany but without figuring a specimen. He believed that it occurred rarely in the Tourtia of Essen, but was found commonly in the Tourtia of Dresden.

Quenstedt (1871) described the German '*T.*' *capillata* d'Archiac as usually small, with a short beak and hardly any folding. He figured a specimen which was small, with a small erect beak, small foramen, depressed shell, and gently uniplicate anterior commissure. The ornament is capillate. No German specimens have been available for sectioning, and although the external morphology would appear different from most Belgian specimens, it is thought wise to retain these specimens within *P. capillata* (d'Archiac) for the present.

Platythyris diversa sp. nov.

Plate 42, figs. 3–6; text-figs. 11, 13*a–c*

1903 *Terebratula capillata* d'Archiac; Lamplugh and Walker, p. 249, pl. 16, figs. 1*a*, *b*.

Diagnosis. Ventral profile circular, oval or pentagonal-oval. P/A ratio about 1. Beak sub-erect or erect; beak ridges usually well defined. Foramen large, circular, mesothyrid, or permesothyrid; telate, attrite, marginate, or labiate. Symphytium, short, wide, 'narrow-waisted'. Anterior commissure rectimarginate to strongly uniplicate. Hinge plates fairly wide, horizontal, tapering; becoming cuneate, keeled in gerontic stage. Anterior free extension of hinge plates very narrow with square cross-section. Crural processes low, pointed, strongly curved inwards. Loop narrow.

Holotype. BM BB76242, from the Shenley Limestone. Dimensions: length 23·5, width 22·0, thickness 10·5.

Description. This species has a very wide range of external form, with differences in the proportions of length, width, and thickness. Representative variations are shown in Pl. 42. The characters of beak and foramen are fairly constant, but some individuals have long, nearly straight beaks with small foramina. Labiate foramina are rare in the Shenley Limestone representatives of the species, but are common in those of the Red Rock, which appear sufficiently distinctive to form a separate subspecies, described below. An extreme variety from the Shenley Limestone has a pentagonal ventral profile (Pl. 42, fig. 4), the brachial valve more obese than the pedicle valve, and the anterior commissure strongly uniplicate. These individuals bear a strong resemblance to *Walkerithyris mendax*, but the distinctive capillate ornament and tapering, horizontal hinge plates revealed by sectioning show the true taxonomic position of these individuals.

Juveniles all have depressed shells and rectimarginate anterior commissures. Slight uniplication may develop at an early stage.

EXPLANATION OF PLATE 42

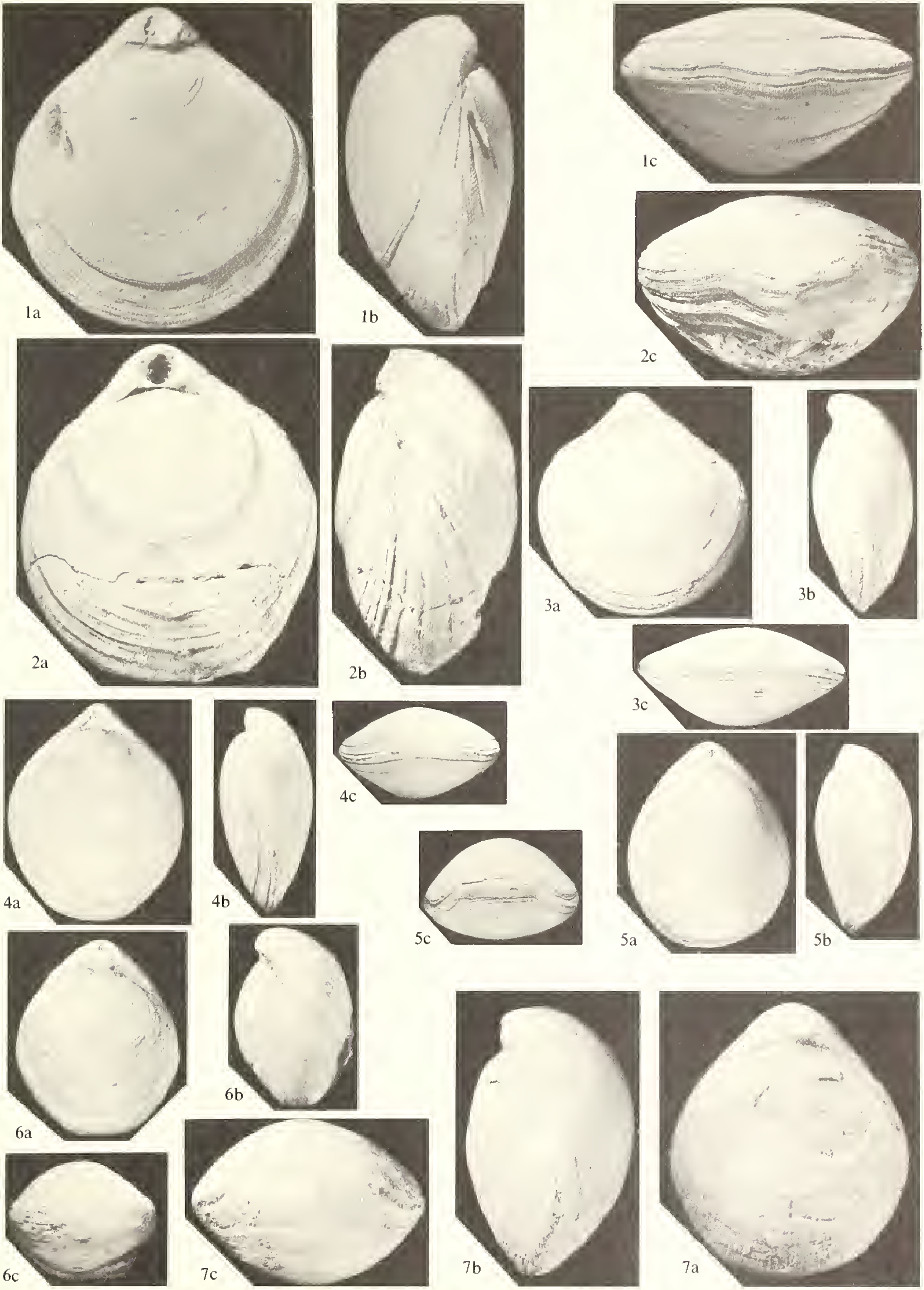
All figs. × 1·5.

Figs. 1, 2. *Platythyris capillata* (d'Archiac), Tourtia (Cenomanian), Tournai, Belgium. 1*a–c*, Neotype, M.T.C. 10156. 2*a–c*, a gerontic specimen, BM B46351.

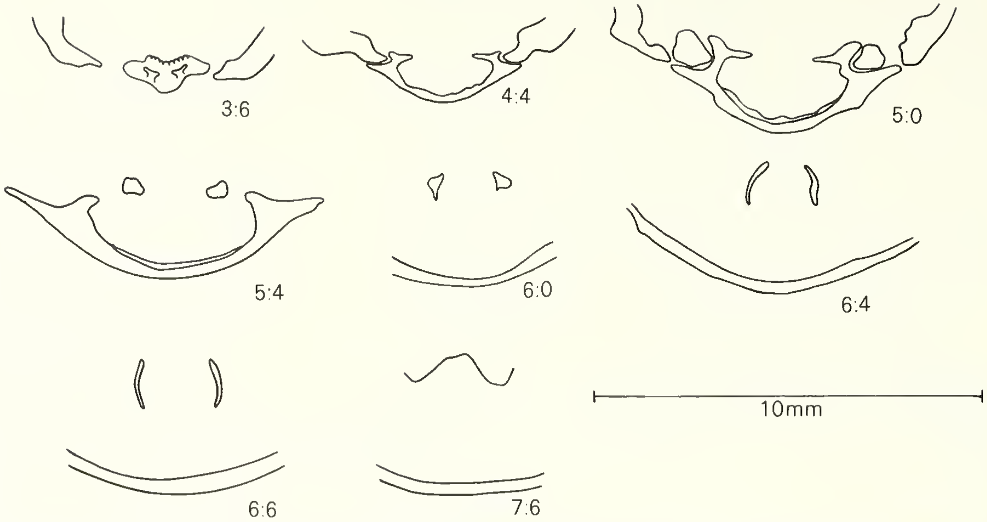
Figs. 3–6. *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. 3*a–c*, Holotype, BM BB76242. 4*a–c*, a small oval, very gently uniplicate specimen, BM 20061. 5*a–c*, a uniplicate specimen similar in external form to *Walkerithyris mendax*, BM 8539. 6*a–c*, a small, obese specimen approaching *P. diversa rubicunda*, BM BB76243.

Fig. 7*a–c*. *Platythyris diversa rubicunda* subsp. nov., Red Rock (Upper Albian), Hunstanton, Norfolk. Holotype, BM BB4191.

PLATE 42



COX and MIDDLEMISS, Cretaceous Terebratulacea



TEXT-FIG. 11. Transverse sections through *Platythyris diversa* sp. nov. The horizontal, tapering hinge plates are seen at 3·6–5·0, the subrectangular free bases of the crura at 6·0, the close-set, incurving crural processes at 6·4, and the low-arched transverse band at 7·6. BM BB76253, Shenley Limestone, Leighton Buzzard.

Remarks. This species was described by Lamplugh and Walker (1903) who identified it as *T. capillata* d'Archiac, and acknowledged the wide range of external features. They had at their disposal a wide selection of Tourtia material for comparison with that from Shenley, but could not separate them taxonomically. Many of the Shenley Limestone specimens in the British Museum collections are, in the main, almost identical in external form with the specimen figured by d'Archiac (1847, pl. 20, fig. 1) but are always smaller, have slightly wider, less produced beaks, and remain rectimarginate to uniplicate. Certain generalizations can be made on the difference between the two species.

The Tourtia species *P. capillata* reaches a generally greater size than the English Albian species *P. diversa*, and it may be slightly sulciplicate or sulcate when fully mature. The internal characteristics show certain differences. The descending branches of the loop of *P. diversa* diverge less than those of *P. capillata*. The hinge plates of both species are horizontal and tapering, becoming cuneate and keeled in old age. Those of *P. capillata* are narrower, thicker, and taper less gradually than those of *P. diversa*.

The horizontal, tapering hinge plates of *P. diversa* resemble those of *P. comptonensis* Middlemiss from the English Aptian but other internal features are different. The loop in *P. comptonensis* is narrower and the inner socket ridges make a much deeper angle with the hinge plates. Externally, some individuals of both species may resemble each other but they have different ornament, and *P. comptonensis* has sharper beak ridges and a lower angle of truncation of the beak.

In the Sedgwick Museum there are two specimens with the external form and ornament of *P. diversa*. These are said to have come from the Aptian of Upware and were collected by Keeping. The Aptian deposits of Upware are no longer exposed and there is some doubt about the exact limits of their age, but if these specimens are in fact from the Aptian the range of the species could be at least that old.

The name of this species refers to the diversity of the external form.

Platythyris diversa rubicunda subsp. nov.

Plate 42, fig. 7; text-figs. 12, 13*d–f*

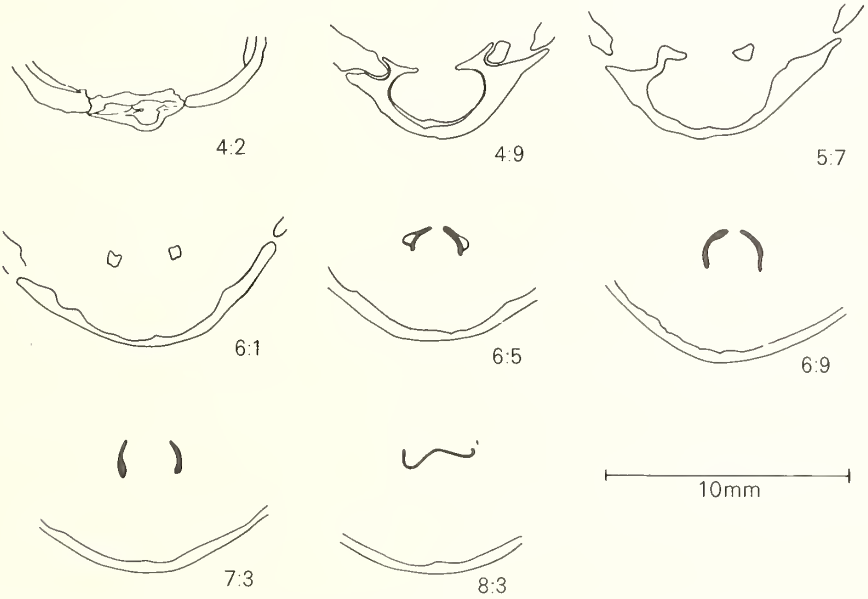
1852 *Terebratula capillata* d'Archiac; Davidson, p. 46, pl. 5, fig. 12.
1874 *Terebratula capillata* d'Archiac; Davidson, p. 33, pl. 17, fig. 2.

Diagnosis. Platythyris diversa of oval or pentagonal ventral profile, obese as adult; beak short, thick; foramen commonly labiate; anterior commissure rectimarginate or uniplicate.

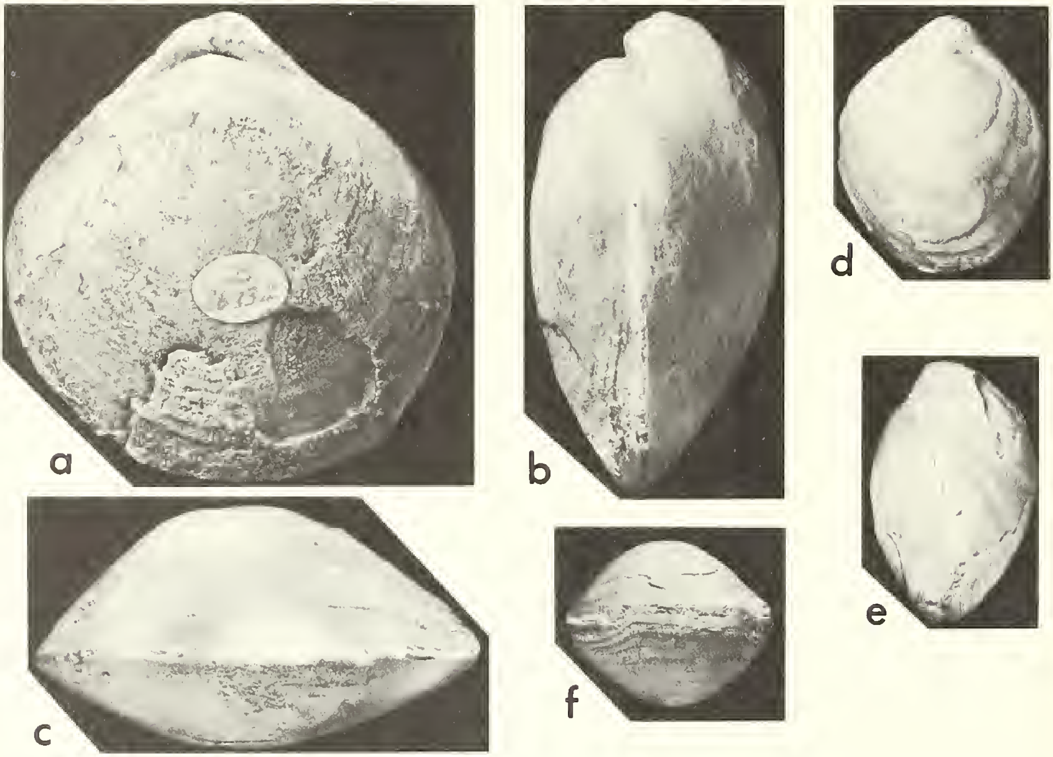
Holotype. BM BB4191 from the Red Rock of Hunstanton, Norfolk. Dimensions: length 28·5, width 25·0, thickness 18·0.

Range. Albian.

Remarks. The external features of *P. diversa* from the Red Rock are sufficiently distinctive to justify the erection of a separate subspecies, which is described here for completeness, although specimens from the Shenley Limestone which show similar features are rare.



TEXT-FIG. 12. Transverse sections through *Platythyris diversa rubicunda* subsp. nov. The horizontal, tapering hinge plates are seen at 4·2 and 4·9, the subrectangular free bases of the crura at 6·1, the close-set incurving crural processes at 6·9, and the low-arched transverse band at 8·3. BM BB76254, Red Rock (Upper Albian), Speeton, Yorkshire, except for section 4·2, which is from BM BB76255, Red Rock (Upper Albian), Hunstanton, Norfolk.



TEXT-FIG. 13. *a–c*, *Platythyris diversa* sp. nov., Shenley Limestone, Leighton Buzzard. A gerontic specimen. BM B26334. × 1·5. *d–f*. *Platythyris diversa rubicunda* subsp. nov. Red Chalk (Upper Albian), North Grimston, Yorkshire. BM BB76244. × 1·5.

The obese shell and labiate foramen are characteristic of the majority of individuals of this subspecies from the Red Rock of Norfolk, Lincolnshire, and Yorkshire. A minority of individuals, more like the Shenley members of the species, are less obese and lack the labiate foramen.

Davidson (1852) described this subspecies from the Red Rock as *T. capillata* d'Archiac, but later (1874) suggested that perhaps the specimens may have constituted a different species or subspecies of *T. capillata*. He was, of course, unaware of the Shenley Limestone fauna which was not discovered until 1903.

The oval ventral profile, obesity, and the relatively large size which some individuals may attain, give this subspecies a closer similarity to *P. capillata* var. a. from the Tourtia of Tournai than any of the Shenley Limestone members of this species. The hinge plates of some individuals of the subspecies are narrower and thicker than is typical for *P. diversa*, and approach the form of those of juvenile *P. capillata*. The name of the subspecies refers to the red colour of the shell, derived from the Red Rock matrix (Albian) of Hunstanton, Norfolk, and to the obese shape of the typical form.

CONCLUSIONS

The stratigraphical and geographical isolation of the Cretaceous brachiopod-bearing beds makes stratigraphical conclusions difficult to draw from the study of the Terebratulacea. Nevertheless, it is possible to make some comparisons between the Shenley Limestone fauna and that of other Cretaceous horizons. Middlemiss (1959) considered the Aptian and Albian terebratulacean faunas as distinct, but the present work on the Shenley Limestone fauna indicates that the distinction is not absolute. Owen (1960) came to a similar conclusion when considering the Cretaceous rhynchonellid genus *Cyclothyris*, although the English Cretaceous rhynchonellids have a wider distribution than the terebratulaceans. When the English Aptian and Albian are compared, it is evident that some Aptian genera are absent from the Albian. *Cyrtothyris* and *Praelongithyris* are absent from the Shenley Limestone, although *Rectithyris shenleyensis* is probably related to the former genus. *Rhombothyris* is not found in the Shenley Limestone and seems to have disappeared at the end of the Aptian. Rare individuals of *Sellithyris* cf. *sella*, a typical Aptian species, occur in the Shenley Limestone. Specimens labelled *T. capillata* in the Keeping Collection from the Upper Aptian, Upware, Cambridgeshire, now in the Sedgwick Museum, Cambridge (SM B2543-40), suggest the possible occurrence of *P. diversa* in the Aptian. Poorly preserved specimens similar to *Boubeithyris boubei* are in the British Museum and Sedgwick Museum collections from the Upper Aptian of Seend, Wiltshire (BM 88829; SM B28131-2). This is probably the first appearance of an Albian-like brachiopod fauna in the Aptian. *W. mendax* does not appear in the English Aptian but this has already been discussed as a peculiarly isolated species that appears to be confined to the Shenley Limestone. The base of the Gault near Leighton Buzzard, at Billington Crossing and Chamberlain Barn pits, contains a fauna of phosphatized Terebratulacea similar to the Shenley Limestone fauna, including *B. boubei*, *W. mendax*, and *P. diversa*.

Other English Albian beds contain a somewhat different terebratulid fauna; for example the commonest biplicate species in the Red Chalk, Upper Greensand, and Gault *Moutonithyris dutempleana* (d'Orbigny), does not occur in the Shenley Limestone. Neither does another biplicate species, the small '*T.*' *biplicata* Sowerby, which is known from the Warminster Greensand (Cenomanian) and occasionally the Upper Greensand. *W. mendax*, *B. boubei*, and *B. buzzardensis*, on the other hand, all occur in the Shenley Limestone but not in the remainder of the English Albian. These differences are probably a reflection of differences in environment and the numbers of fossils preserved at different horizons. A point of similarity between the Red Chalk and the Shenley Limestone is the presence of *P. diversa*, although the Red Chalk has a different subspecies. *Rectithyris* cf. *shenleyensis* occurs in the Warminster Greensand (Cenomanian). *T. ovata* of the Warminster Greensand is closely related to *B. boubei* of Shenley.

The similarity between the Belgian Tourtia (Cenomanian) terebratulacean fauna and that of the Shenley Limestone is not as great as Lamplugh and Walker (1903) supposed. They have only one species, *B. boubei*, in common. *R. depressa*, *P. capillata*, *T. robertoni*, *T. crassa*, *T. tornacensis* and other species illustrated by d'Archiac (1847) are absent from the Shenley Limestone. Typical Shenley Limestone species which are absent from the Tourtias are *R. shenleyensis*, *P. diversa*, *B. buzzardensis*, and *W. mendax*. The faunas are related at the generic level but the superficial similarity of the species is probably the result of the similar environments suggested by the lithological similarity of the matrices. In conclusion, the evidence suggests that the Shenley Limestone (Lower Albian) terebratulacean fauna is transitional between Aptian and Cenomanian faunas.

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The text figures have been redrawn from Dr. Cox's originals by Miss M. L. Holloway of the British Museum (Natural History), and photography is by the photographic department of the Museum.

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LATE CRETACEOUS COPROLITES FROM WESTERN CANADA

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ABSTRACT. Abundant coprolites and possibly gut fills of holostean fishes are irregularly distributed throughout the kaolinitic clays and muds of the Whitemud Formation (late Cretaceous) of the Willows-Readlyn district, south-central Saskatchewan. The coprolites show a variety of internal and external structures including coiling, folding, and contraction marks of primary origin; secondary features, for example surface cracking, due to diagenetic replacement by siderite and pyrite, and subsequent alteration to iron oxides.

KAOLINITIC silts, muds, and clays, commonly light grey to white in colour, are characteristic of the nonmarine Whitemud Formation (late Cretaceous) in the type section of that unit, exposed near Eastend in the Cypress Hills region of south-western Saskatchewan (Kupsch 1956). The formation is well exposed further east in broad, deepened valleys, excavated below the general level of the northern Great Plains. This paper describes the first evidence of vertebrate life from this formation: abundant coprolites occurring in the Whitemud strata of south-central Saskatchewan as coiled and related forms of ironstone bodies.

The few specimens previously described as fossilized vertebrate excrements in the late Cretaceous strata of the northern Great Plains regions are of morphologically simple, for the most part broadly ellipsoidal forms, with the composition of apatite known from the Oldman Formation (Campanian) of southern Alberta (Waldman 1970; Waldman and Hopkins 1970).

The discovery of abundant coprolites, possibly tens of thousands of specimens of vertebrate origin in the Whitemud Formation (late Cretaceous) exposures of south-central Saskatchewan is important, in that these deposits have previously yielded only scarce molluscan remains and plant megafossils. The abundance of the coprolites, considered here, has effectively downgraded the economic potential of an otherwise valuable deposit of ceramic clay. The origin and mode of preservation of coprolites from the Whitemud sediments are discussed, with particular reference to external morphology and composition and the environment of deposition of the enclosing sediments.

COPROLITE LOCALITIES

Worcester (1950) describes the economic potential of the kaolin beds, but notes that their utilization is limited by an abundance of 'concretions' 'of odd shape, many as coils, ... not uniformly distributed' in clay pits, located about midway between Willows and Readlyn in the southern half of Section 33, Township 7, Range 28, West of the Second Meridian. Worcester (1950) also noted the occurrence of ironstone concretions

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in the Medalta pit, 3 km north-east of Willows in the north-east quarter of Section 1, Township 8, Range 29, West of the Second Meridian.

These coprolite localities incorporate several abandoned kaolinite pits approximately 3 km north and east of Willows. Approximately 7 m of gently south-east-dipping Whitemud strata are exposed.

The coprolites are readily found, where they have weathered out of the poorly exposed strata. Talus and slope wash concentrations are often as dense as 200 specimens per square metre along a 200 m escarpment. Specimens were not visible in the Whitemud outcrops, adjacent to the immediate collecting area. Extensive slumping and weathering of the bluff face presented difficulties in ascertaining the spatial distribution of the coprolites within the sediments. They are randomly distributed, both horizontally and vertically in the Whitemud section at this locality.

TAXONOMIC DESCRIPTION

The coprolites from the Whitemud Formation are described on the basis of their gross morphology, external and internal, and by small-scale features such as surface ridge patterns and constrictions.

Gross morphology and size. Limonitic coprolites from the Whitemud Formation from the Willows localities are illustrated in Plate 43. An emphasis is placed on illustration of small-scale surface features, both organic and inorganic in origin.

The coprolites exhibit a limited number of morphologic forms. Relatively small (up to 6 cm long) spindle-shaped and segmented, elongate forms (Pl. 43, figs. 1, 2) account for up to 40% of the sample populations. Larger (1·5 to 22·0 cm long) forms, exhibiting spiral and helicoidal coils (Pl. 43, figs. 3–6), and consisting of irregularly contorted masses, resembling piles of lobate segments (Pl. 43, figs. 7–9) account for a further 40%. These morphologic forms may be obscured to varying degrees by irregular, knob-like encrustations of limonitic minerals, which may blanket the entire coprolite, reducing the sharpness of the form (Pl. 43, figs. 10–13). In other specimens, small-scale morphologic features of organic origin extend from within concretionary limonitic masses, as shown in Plate 43, fig. 14.

Constrictions. Both the spindle-shaped and coiled coprolites exhibit usually abrupt constrictions (Pl. 43, figs. 15, 16), which in each case represent a reduction in diameter of the coprolite to less than one-half of the average value, over a distance of a few millimetres along the direction of elongation. In other cases, the coprolites terminate with sharply pointed extremities (Pl. 43, figs. 17, 18).

Most coprolites obscured by concretionary processes retain at least one faint yet diagnostic feature, for example, the extrusive pinch-out of sphincter muscle contractions on the irregular and concretionary spheroid specimen (Pl. 43, fig. 5; arrow).

Perforations. Scarce, subcircular perforations, up to 1·5 mm in diameter and 1·0 cm or more deep, were observed on several coprolites belonging to the main morphological types.

Surface ridge patterns. Relatively smooth surfaces of coprolites from the Whitemud Formation frequently exhibit patterns of delicate ridges and striations (Pl. 43, figs. 19–24). These features are aligned parallel (Pl. 43, figs. 19, 20) or oblique (Pl. 43, fig. 21) to the long axes of straight, spindle-shaped and irregularly coiled forms, and are approximately transverse to the long axes of spirally and helicoidally coiled forms (Pl. 43, figs. 22, 23).

Polygonal patterns of cracks. Relatively smooth surfaces (Pl. 43, fig. 24) are infrequently seen and commonly Whitemud coprolites of all morphological types are transected by polygonal patterns of cracks. These impart a rough, broken, and frequently blocky appearance to the coprolites (Pl. 43, figs. 25–27).

Internal structure. Polished sections through coprolites from the Willows locality frequently reveal finely amorphous limonite, displaying considerable homogeneity in total absence of any internal layering. In a few cases, however, limonite forms a rind around an unreplaced sideritic core (Pl. 44, figs. 1, 2). Somewhat more complex internal structures characterize spirally coiled forms (Pl. 44, fig. 5) and limonitic bodies with extensive concretionary growth (Pl. 44, fig. 7).

Some of the limonitic bodies displaying extensive concretionary growth, with little or no surface evidence of an initial excremental origin, have a confused internal structure with no obviously coprolitic core.

The Whitemud coprolites in thin section are composed of amorphous limonite, frequently forming flattened, ovoidal bodies (Pl. 44, fig. 6).

Incorporated organic material. Isotropic, lath-like bodies which may be limonite-replaced plant fragments are fairly common within some coprolites (Pl. 44, fig. 4). Impressions after plant fragments, up to several centimetres in length, adhering to the outer surfaces of coprolites are common to all morphological types (Pl. 43, figs. 8, 10).

MINERALOGY

The original faecal material was totally replaced by siderite and pyrite, which were subsequently replaced by limonite, goethite, and lepidocrocite, partially to completely during the oxidizing environment of kaolinization of the feldspathic sand and diagenetic recrystallization of the kaolinitic detritus.

Three random samples, representative of major morphological categories, were selected for detailed mineralogical and geochemical examination:

A. Linear, rounded cross-section, irregularly ribbed, finely striated, terminal twist and constriction, with minor constrictions of one inch apart. Over-all length of 6·0 cm; maximum width of 2·5 cm.

B. Spirally coiled, with rounded cross-section, finely striated; surface blocky, because of polygonal fracture pattern. Over-all, coiled length of 7·5 cm; maximum width of 6·0 cm.

C. Irregular morphology, with coils largely obscured by concretionary growth; pustulate surface. Over-all length of 9·5 cm; maximum width of 7·5 cm.

The X-ray powder diffraction of the three samples indicates the coprolites to be composed of iron oxides and carbonate: goethite, lepidocrocite, and siderite. The presence of siderite was also confirmed by the exothermic reaction of the D.T.A. occurring between 350 °C and 500 °C, as well as the weight loss over the same range on the T.G.A. The major endothermic D.T.A. reactions between 200 °C and 350 °C are in agreement with the X-ray diffractometer identification of the various forms of goethite.

The degree of crystallinity of the siderite is believed to be inhibited, which is reflected by the subdued diffractogram peaks as well as by the T.G.A. and D.T.A. data. The thermal decomposition of the structure is between 350 °C and 500 °C, compared to end-member siderite decomposition of 580 °C. Total oxide analyses for three samples were carried out in a standard HF acid bath. Approximately one-half of the original material remained, and this residue was converted to a soluble chloride with hydrochloric acid. The balance in the mineral analyses were considered as oxides since X-ray diffractometer studies indicated the lack of any crystalline minerals, in addition

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EXPLANATION OF PLATE 43

All figures × 0·5.

Fig. 1. Spindle-shaped coprolite, transected by polygonal pattern of cracks.

Fig. 2. Segmented, elongate coprolite, showing pattern of fine surface ridges and striations. The partial twist is transitional from the untwisted linear form of fig. 1.

Fig. 3. Spirally coiled coprolite, displaying irregular cracks at surface. The full coil is transitional from the incomplete coiled form of fig. 2.

Figs. 4–6. Spiral and helicoidal forms: note the progressively diminishing diameter with each coil of the spiral forms (fig. 4) but the nearly consistent diameters of the helicoidal forms (figs. 5, 6).

Fig. 7. Piled, lobate coprolite with concretionary growth masking surface features.

Fig. 8. Piled, lobate coprolite. Arrow indicates surface occurrence of plant fragment.

Fig. 9. Irregularly folded coprolite with surface ridges and striations.

Fig. 10. Irregularly folded coprolite. Arrow indicates plant fragment.

Figs. 11, 12. Spirally coiled coprolites with gross morphology partly obscured and surface detail obliterated by concretionary growth.

Fig. 13. Irregular limonitic body of dominant concretionary origin. These bodies, however, may retain a single organic origin feature, such as a terminal neck (fig. 14).

Fig. 14. Coprolitic surface detail preserved amid concretionary mass (arrow).

Fig. 15. Spindle-shaped coprolite with prominent sphincter-pinched constriction.

Fig. 16. Spirally coiled coprolite with sphincter-pinched constriction and termination (arrow).

Fig. 17. Large, spindle-shaped coprolite with sphincter-pinched termination. Note rough surface.

Fig. 18. Irregularly folded coprolite with polygonal pattern of surface cracks and sphincter-pinched termination.

Fig. 19. Elongate coprolite with longitudinal striations.

Fig. 20. Irregularly folded coprolite with longitudinal striations.

Fig. 21. Spirally coiled coprolite with oblique striations.

Fig. 22. Spirally coiled coprolite with transverse striations.

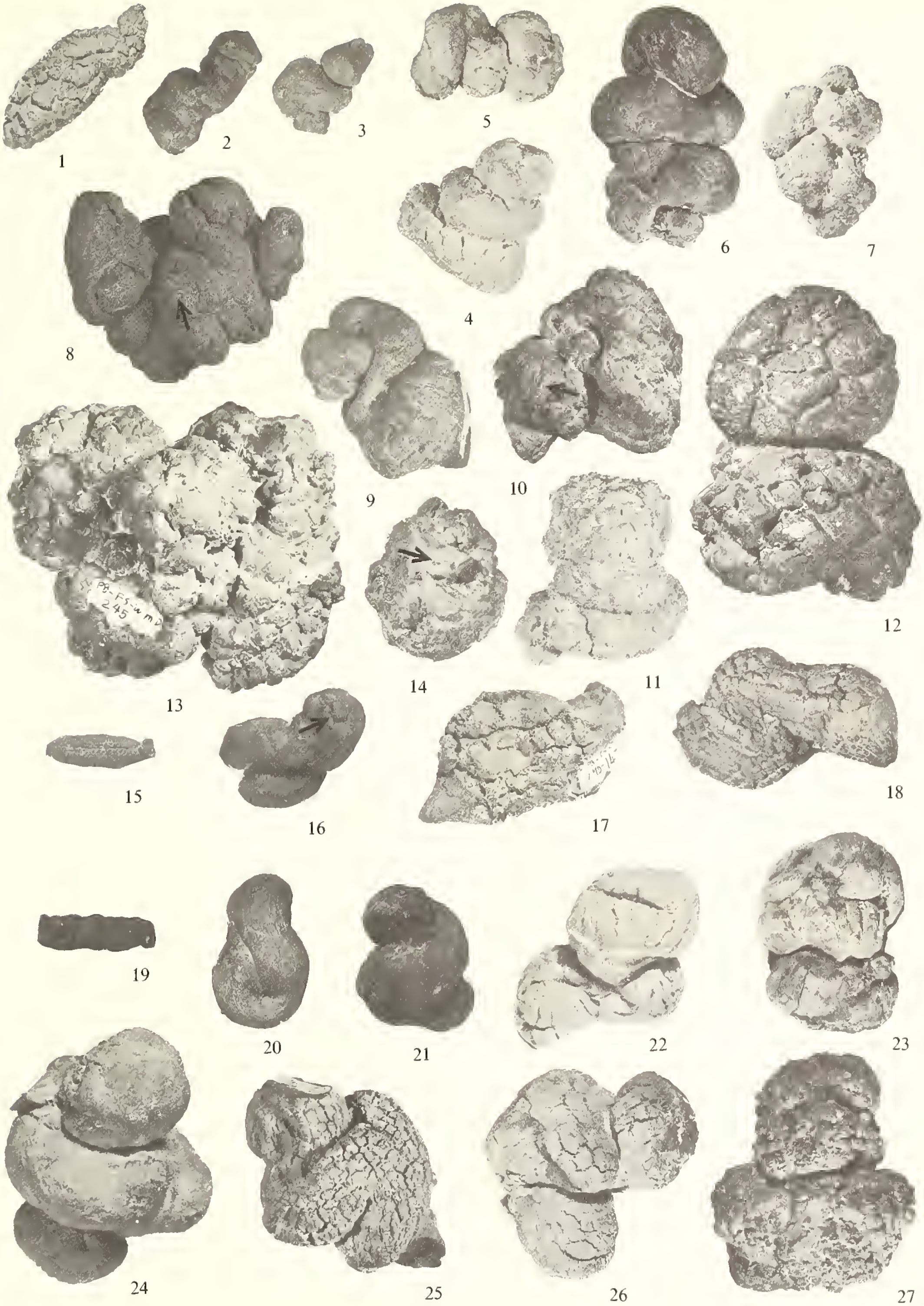
Fig. 23. Irregularly folded coprolite with transverse striations.

Fig. 24. Spirally coiled coprolite with smooth surface.

Fig. 25. Irregularly folded coprolite with surface broken by polygonal pattern of cracks.

Figs. 26, 27. Spirally coiled coprolites displaying polygonal patterns of surface cracks. The delicate muscle striations on the surface are obscured by the crack systems.

All figured specimens are deposited in the collections of the Saskatchewan Geological Survey, Subsurface Geological Laboratory, Regina.



BROUGHTON, SIMPSON, and WHITAKER, fish coprolites to the observed iron oxides and carbonate. The oxide analyses of the three samples are expressed as calculated mineral percentages in Table 1.

Most coprolite specimens have two or more composite, concretionary layers of dark greyish-blue colour, in sharp contrast to the adjacent ochre yellow, light to dark brown, and hematitic red zones. X-ray examination of the major colour zones failed to distinguish any major mineralogical variation. Relict preservation of minor amounts of pyrite in many specimens was observed. The possibility that the dark greyish-blue zones were directly related to the presence of vivianite or another phosphate compound was discounted.

It is thus concluded that the original faecal material was likely replaced by pyrite and siderite, subsequently partially replaced by hydrous iron oxides after burial.

TABLE 1. Mineralogical compositions of representative coprolites calculated from wet chemical oxide analyses. For discussion see text.

		Specimen		
	Composition	A (Linear)	B (Spiral)	C (Concretionary)
Wt % of total sample	Goethite α $Fe_2O_3H_2O$	88·6	69·1	81·0
	Lepidocrocite γ $Fe_2O_3H_2O$	3·7	11·2	0·0
	Siderite $FeCO_3$	4·1	15·7	14·7
	Oxides	1·3	1·5	3·1
	Organics	0·2	0·1	0·1
	H_2O	1·6	1·7	0·9
	Total	99·5	99·3	99·8

EXPLANATION OF PLATE 44

Figs. 1, 2. Thin sections through irregularly coiled coprolites. Negative prints show rings of limonite (light) surrounding sideritic cores (dark) in sharp contact (fig. 1) and in gradational to irregular contact (fig. 2), × 2·3.

Fig. 3. Intricate, internal folds observed in longitudinal section through the spiral coprolite, of fig. 5 (this plate). Probably preservation of the gut and unexpelled excrement, × 40.

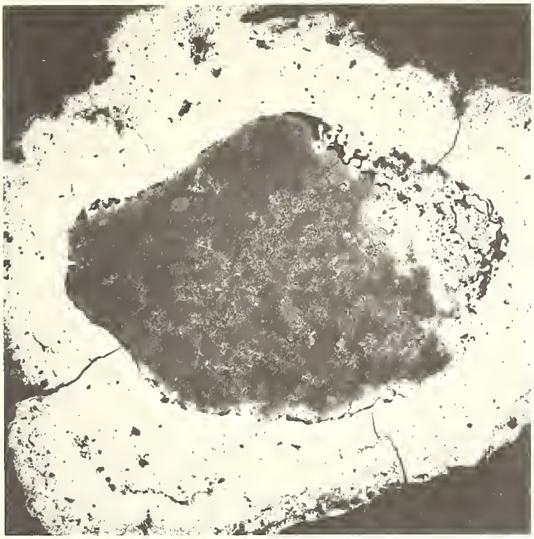
Fig. 4. Amorphous limonite and plant fragment internal to the coprolite, × 40.

Fig. 5. Polished longitudinal section through a spiral coprolite. The internal folds may represent preservation of the gut tissue and unexpelled excrement. Compare with the irregular texture of expelled excrement of fig. 7, × 0·5.

Fig. 6. Secondary amorphous limonite deposited as flattened ovoidal mosaics, a texture representative of expelled excrement, × 40.

Fig. 7. Polished section through irregular faecal mass with the obscuring effects of the concretionary and amorphous ovoidal limonite bodies, × 0·5.

All figured specimens are deposited in the collections of the Saskatchewan Geological Survey, Subsurface Geological Laboratory, Regina.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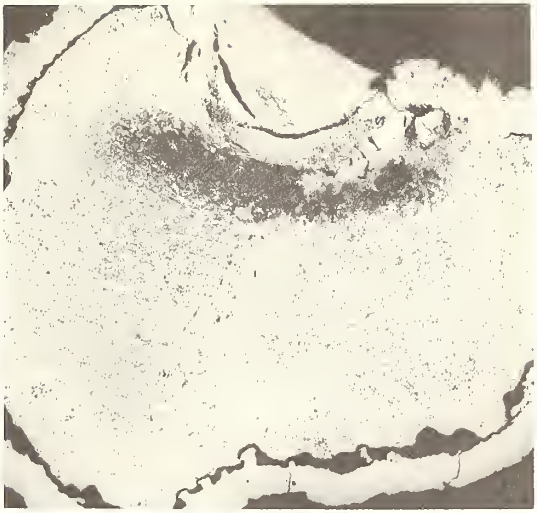
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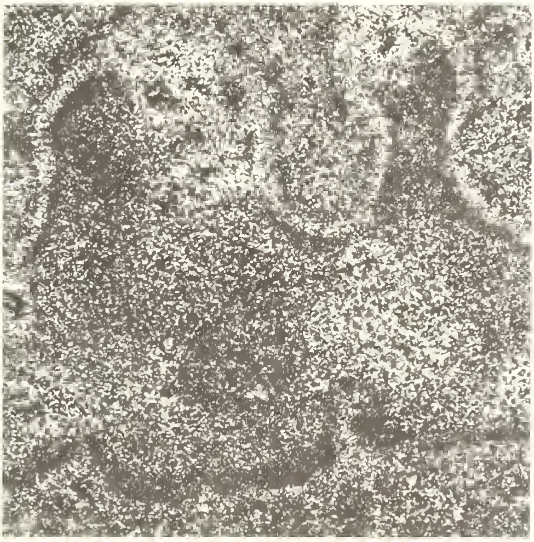
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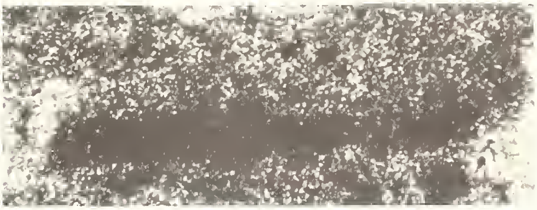
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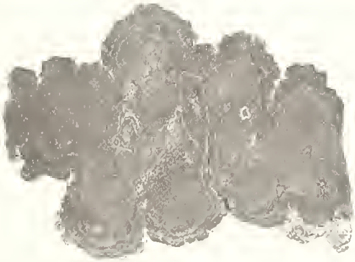
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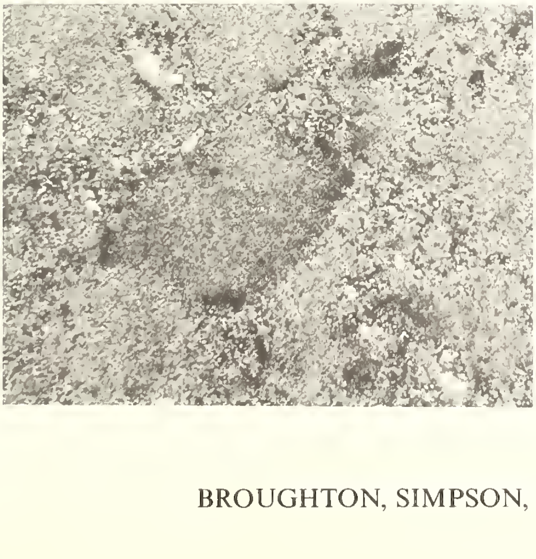
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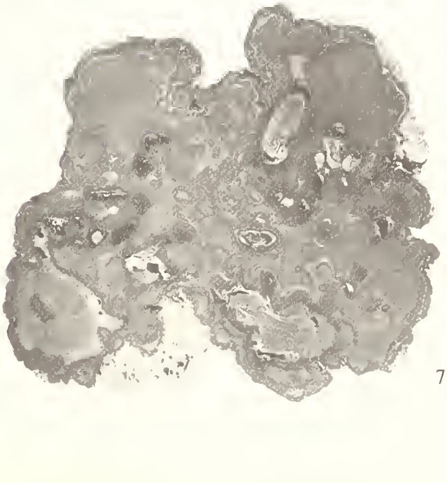
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BROUGHTON, SIMPSON, and WHITAKER, fish coprolites

DISCUSSION

Organic and inorganic origin of structural features

Amstutz (1958) was much impressed by the morphologies, displayed by Tertiary coprolites from Washington, to the extent that he wrote, '... the shapes do not leave any doubt as to their true animal excrement origin' and 'if it were not for the hardness, they could be taken for true excrements'. Much the same kind of sentiment might be expressed about the general gross external morphology of the limonitic bodies from the Whitemud Formation. However, the specimens exhibit transitions in the general morphology from excrements with preserved original surface details, although dung-like forms with varying degrees of obscuring limonitic encrustation to irregularly pustulate concretions, with little or no resemblance to cropolites.

The constrictions and striations that characterize the external surfaces of many specimens are undoubtedly of organic origin. These features are thought to have resulted from localized squeezing of the excrement, attendant upon contraction of the sphincter muscles during defaecation. The ridges and striations are thought to be the impressions of intestinal and sphincter muscles. The few irregular limonitic bodies, characterized by apparent dominance of concretionary growth may have originated as gastric residues or irregular faecal masses, similar to those described by Zangerl and Richardson (1963).

Perforations on the surface of some specimens may be gas-escape features, such as those described from coprolites by Jepsen (1963) and Zangerl, Woodland, Richardson, and Zachry (1969).

Hantzschel, El-Baz, and Amstutz (1968) have noted that the spiral form of some coprolites is regarded as a diagnostic feature of an excremental origin. Many specimens exhibit evidence of a spiral valve within the gut of the animal. The spiral coprolites frequently exhibit an intricate internal folding, similar to that figured by Williams (1972) and interpreted by him as representing mucosal folds of a shark's intestine. This suggests that at least some of the Whitemud coprolites are fossilized intestines and not expelled excrement. In a study of spiral coprolites from the Lower Permian Wymore Shale of Kansas, Williams (1972) concluded that the faecal masses are the fossilized intestines of pleuracanth sharks. Williams (1972) examined thin sections of the coprolites, which revealed structures analogous to mucosal folds of the intestine. Comparable features are rare in the Whitemud coprolites, but have been observed in a few cases (Pl. 44, fig. 3). Zangerl and Richardson (1963) adopted the view that the plasticity of faeces at the time of extrusion controls to a large extent the gross morphology of the resulting dung deposit. Thus, excrement extruded from the lower intestine into the rectum will roll into a coil at particular optimum plasticity, while deviations from that plasticity will produce irregular coiling or lack of spiral structure. This fact may account for the existence of uncoiled coprolites with similar 'primary' surface features to those of coiled ones also occurring in the Whitemud Formation. However, different coprolite morphologies, possessing essentially similar, small-scale, surface ridge patterns, may also represent droppings from different phases within a single episode of excretion, comparable to the fore, middle, and end droppings, distinguished by Kao (1962). The common occurrence of an outer sheath of embedded plant remains on coprolites of all types suggests that the majority was expelled on to a subaqueous depositional surface, strewn with plant debris. As noted above, the internal structure of some spirally and helicoidally coiled coprolites without a sheath of plant debris indicates that these may be the fossilized intestines of fishes.

It is likely that the density and depth of penetration of patterns of cracks on the surface of the coprolites are functions of the original composition and consistence of the faecal masses at the time of extrusion, as well as of physiological factors controlling the rate of extrusion. Many of the polygonal patterns of cracks, by analogy with similar fracture systems, developed around the sideritic concretions, described by Franks (1969), are a consequence of a synaeresis. Indeed, Conybeare and Crook (1968, pl. 47A, p. 177) figure a clay-siderite coprolite showing synaeresis cracks. Zangerl and Richardson (1963) suggest that larger cracks may have served as degassing channels during anaerobic decomposition of the faecal masses, because of accumulations of sulphides where the cracks make contact with the shales surrounding the coprolites. An association of pyrite crystals with some of the larger surface cracks on Whitemud coprolites indicates that this argument might be equally valid in the specimens considered here.

Possible systemic affinity. The meagre fossil record of the Whitemud Formation in southern Saskatchewan and, in particular, the lack of any finds of vertebrate body fossils precludes interpretations without uncertainty.

The spirally and helicoidally coiled appearance of many Whitemud coprolites, and the large sizes frequently encountered, suggest the possibility of activity of fishes among the larger elasmobranchs. The gut of the elasmobranchs is characterized by a short intestine, the surface of which is greatly increased by the presence of a spiral ridge or valve and also a strong pyloric sphincter marks the junction between stomach and intestine (Young 1962). Presence of a spiral, intestinal value in the animal of origin is essential in the production of coiled coprolites, regardless of whether extruded faeces (Zangerl and Richardson 1963) or unexpelled excrement (Williams 1972) is under consideration. Large size of coprolites has been a significant factor in arguments, to the effect that sharks were the animals of origin for such coprolites (Zangerl and Richardson 1963). This interpretation was favoured in a preliminary discussion of the Whitemud specimens by Broughton, Simpson, and Whitaker 1974).

A. Jerzmanska of the University of Wrocaw, Poland, pointed out (pers. comm. 1976) that such a narrow interpretation of possible animals of origin is perhaps ill-advised, since several other major groups of fishes possess spiral valves and representatives of some of these groups have been recorded from the Cretaceous rocks of the northern Great Plains of North America. Actinopterygian fishes of the Superorder Chondrostei, possessing spiral intestinal valves, included *Polypterus* (the bichir) and *Acipenser* (the sturgeon), while the Superorder Holostei includes *Lepisosteus* (the garpike) and *Amia* (the bowfin), which have somewhat reduced spiral valves (Young 1962). Furthermore, the sarcopterygh Order Dipnoi (lung-fishes) have spiral valves and do not excrete spirally coiled faecal masses (Williams 1972).

Of these several possibilities, sturgeons and bowfins constitute the most likely animals of origin for the Whitemud coprolites. MacAlpin (1947) recorded the occurrence of *Paleopsephurus wilsoni*, a polyodontid fish (sturgeon), in the upper Cretaceous sediments of Montana, while the presence of *A. frugosa*, also in the Montana Cretaceous, was noted by Boreske (1974).

The possibility that sturgeons produced the Whitemud coprolites is attractive for several reasons, most of which relate to the physiology and mode of life of these fishes, as described by Young (1962). The skull and skeleton are almost entirely cartilaginous and lack teeth development; the dermal skeleton is much reduced. These skeletal features might account for the apparent absence of body fossils of fishes in the Whitemud sequence, although the remarks of Romer (*in* Hantzschel *et al.* 1968) on coprolite and bone occurrences in the Texas Permian succession may be of significance. He noted that coprolites, mostly, if not all, of shark origin, are common in the Permian redbeds, but the bones tend to be relatively scarce and concentrated in pockets. Furthermore, sturgeons live in the sea, but migrate up rivers for breeding and to feed upon invertebrates collected from bottom muds, stirred up by the fishes' snout. This diet might account for the absence of skeletal material in the coprolites; if the latter had been produced by sharks, abundant bones, teeth, and scales would be expected to be incorporated in the faecal masses. Finally, sturgeons attain large dimensions, weighing up to 1000 kg.

CONCLUSIONS

Ironstone bodies, previously interpreted as inorganic concretions, are irregularly distributed throughout the kaolinitic clays, silts, and muds of the nonmarine Whitemud Formation (late Cretaceous) between Willows and Readlyn in south-central Saskatchewan. Gross morphology, surface features, and scarce internal structures indicate that reinterpretation of these bodies as coprolites is warranted. The abundance of the coprolites is such as to downgrade the economic potential of a section of otherwise valuable, ceramic clays.

There is no obvious reason for the concentration of coprolites at this site. It is the opinion of the authors that they form an *in situ* deposit and not a mechanical concentration. The preservation is remarkably good, and the coprolites lack any obvious signs of abrasion, due to transportation by currents. However, some selective erosion of bottom muds by currents, with attendant, minor, vertical displacement of the coprolites remains a possibility.

The coprolites have been preserved as a result of total replacement of the original faecal material by siderite and pyrite, which was subsequently replaced by limonite (goethite and lepidocrocite). A limited number of morphological types was recorded and certain external surface features are common to most of these: (1) sphincter-pinched constrictions and terminal necks; (2) polygonal patterns of cracks, probably of synaeresis origin; (3) patterns of fine ridges and striations, which appear to be intestinal and sphincter-muscle impressions; and (4) perforations of gas-escape origin. These surface features are masked to varying degrees by concretionary growth of limonite around the faecal masses.

The animals of origin of the coprolites were probably sturgeons or bowfins, which are known from the Cretaceous strata of Montana. The Whitemud Formation was deposited in near coastal alluvial floodplain palaeoenvironment.

Evidence of expulsion of the faecal masses from the animals of origin is provided by the fragmental plants adhered to the surface of the excrement upon deposition on to the substrate. Some of the spirally and helicoidally coiled faecal masses may be the fossilized intestines of fishes.

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TYPES OF THE ORDOVICIAN TRILOBITES *CELTENCRINURUS MULTISEGMENTATUS* (PORTLOCK) AND *CRYPTOLITHUS LATUS* PORTLOCK

by S. P. TUNNICLIFF

ABSTRACT. Attention is drawn to a hitherto overlooked note by Portlock, dated 1837, which is of significance to the dates and type specimens of the trilobite species *Celtencrinurus multisegmentatus* (Portlock) and *Cryptolithus latus* Portlock, both of which have been assumed to have dated from Portlock's 1843 Report.

IN the course of curation and cataloguing the Lower Palaeozoic part of the Portlock Collection held by the Institute of Geological Sciences, London, research led to a notice by Portlock published in November 1837, and thus predating the well-known *Report on the Geology of Londonderry, etc.* published in February 1843. The 1837 notice appears at the back of Larcom's memoir on the *Ordnance Survey of the County of Londonderry*. Portlock (1843, p. v) and Andrews (1975, p. 157) both suggest that this work was previously printed for the British Association meeting in Dublin in 1835, but, by Article 9 (2) of the International Code of Zoological Nomenclature, this does not constitute a publication. No copy of this has been traced and circulation was probably very limited, whereas the 1837 version is stated by Andrews (1975, p. 158) to have sold 1,250 copies in six years. However, it has seldom been referred to by subsequent authors.

The 1837 notice includes three plates of fossils, mostly from the Pomeroy area, Co. Tyrone, and introduces two new specific names, *Calymene multisegmentatus* and *Cryptolithus latus*. Both of these species have in the past been taken as dating from the 1843 report, with types recognized accordingly. In both cases the specimens figured in 1837 differ from those figured, with revised generic assignments, in 1843. The specimens figured in 1837 and recognized in the Portlock Collection at the Institute of Geological Sciences, London, are here chosen as lectotypes, being the only certain surviving syntypes, there being no evidence to indicate whether the specimens figured in 1843 were known to Portlock in 1837.

Notes on the specimens

Celtencrinurus multisegmentatus

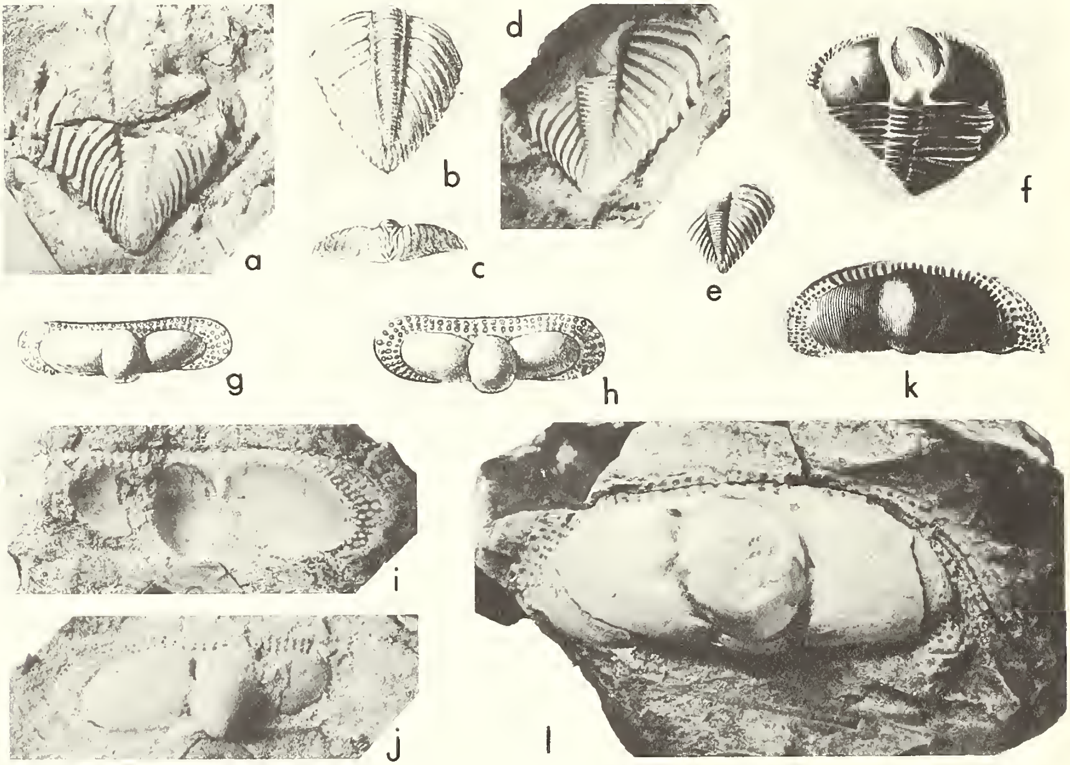
1837 *Calymene multisegmentatus* Portlock, p. 6, pl. 2, fig. 7.
1843 *Ampyx baccatus* Portlock, p. 262, pl. 3, fig. 11.
1843 *Amphion multisegmentatus* Portlock, p. 291, pl. 3, fig. 6*a*, *b*.

[Palaeontology, Vol. 21, Part 2, 1978, pp. 455–458.]

1853 *Encrinurus multisegmentatus* Portlock; Salter, pl. 4, p. 7 (includes both *multisegmentatus* and *baccatus* in *E. multisegmentatus*).
1906 *Encrinurus multisegmentatus* (Portlock); Reed, p. 122.
1957 *Encrinurus multisegmentatus* (Portlock); Tripp, p. 61, pl. 11, fig. 6; pl. 12, figs. 2*a*, *b*, 4, 6.
1977 *Celtencrinurus multisegmentatus* (Portlock); Evitt and Tripp, p. 119.

The Portlock Collection contains one incomplete cranidium of *baccatus*, GSM 35415, stated by Portlock (1843, p. 262) to be his only specimen and therefore the holotype by monotypy of that species.

Three Portlock specimens of *multisegmentatus* are known; GSM 35416, 35417, 35419, all pygidia. Specimen 35417 can be identified as that figured in 1837, while 35416 has long been regarded as that figured in 1843. It must be observed, however, that 35417 bears some resemblance to the 1843 figure if allowance is made for the



TEXT-FIG. 1. *a–e*, *Celtencrinurus multisegmentatus* (Portlock). *a*, GSM 35416, pygidium, × 2. *b*, *c*, reproductions of Portlock's figures of the same specimen (1843, pl. 3, fig. 6*a*, *b*), × 1. *d*, GSM 35417, lectotype, pygidium, × 2. *e*, reproduction of Portlock's figure of the same specimen (1837, pl. 2, fig. 7), × 1. *f–l*, *Cryptolithus latus* Portlock. *f*, reproduction of Portlock's figure of a specimen not now known (1837, pl. 2, fig. 8), × 1. *g*, *h*, reproductions of Portlock's 1843 pl. 1B, figs. 11, 12 respectively, × 1. *i*, GSM 14016, cephalon, the supposed original of Portlock's 1843 figures, × 2. *j*, latex cast from GSM 14016, × 2. *k*, reproduction of Portlock's 1837 pl. 1, fig. 5, × 1. *l*, GSM 14019, lectotype, cephalon, the original of Portlock's 1837 figure, × 2. All specimens are from the Killey Bridge Formation (Ashgill Series, Cautleyan Stage), Pomeroy district, Co. Tyrone.

reconstruction of the left side, Portlock's figure appearing somewhat diagrammatic on that side. Both have been refigured by Tripp (1957, pl. 12, figs. 4, 6), who mistakenly considered 35416 to be the holotype (by monotypy) in the belief that Portlock's description (1843, p. 291) referred to only one specimen (R. P. Tripp 1976, pers. comm.). Portlock's use of the word *neither* in his discussion (1843, p. 291, line 22) indicates that two specimens were available to him in the preparation of the 1843 Report, but the number of specimens available at the time of his preparation of the 1837 paper is not known. GSM 35417 is, therefore, the only certain syntype and as such is designated as lectotype of *Calymene multisegmentatus* Portlock, 1837. The lithology suggests that the specimen is from the Killey Bridge Formation (Ashgill Series, Cautleyan Stage); Pomeroy district of Co. Tyrone, exact locality uncertain.

Cryptolithus latus

1837 *Cryptolithus latus* Portlock, p. 6, pl. 1, fig. 5; pl. 2, fig. 8.
1843 *Trinucleus fimbriatus* Murchison; Portlock, p. 264.
1843 *Trinucleus latus* Portlock, p. 264, pl. 1B, figs. 11, 12 (as *T. fimbriatus* Murchison), Synoptical table p. 753.
1853 *Trinucleus portlockii* Salter, pl. 7, p. 6 (cited only).
1952 *Trinucleus (Cryptolithus) portlockii* Salter; Reed, p. 99.
1975 ?*Cryptolithus portlockii* Salter; Hughes, Ingham, and Addison, p. 594.

Portlock's explanations to his 1837 figures read thus: pl. 1, fig. 5 *Head of trilobite see Plate 2 Fig. 8* and pl. 2, fig. 8 *Cryptolithus latus*; clearly he included both in *latus*. Of the two figured specimens, only the former has been recognized; this is GSM 14019, which as the only known syntype from 1837, is designated as lectotype of *C. latus* Portlock, 1837; Killey Bridge Formation (Ashgill Series, Cautleyan Stage); Pomeroy district of Co. Tyrone, exact locality uncertain. GSM 14016 is the specimen figured in 1843, pl. 1B, fig. 11 and probably fig. 12 despite the confusion shown by Reed 1952, pp. 98–100, where he identified Portlock's figures with specimens GSM 14014, 14016, and 14017 on consecutive pages.

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DO TRILOBITES HAVE A TYPICAL ARTHROPOD CUTICLE?

by KENNETH M. TOWE

ABSTRACT. Problems with specimen preparation and diagenesis make it uncertain whether all trilobites had a laminated cuticle. However, in those trilobites that do show laminations, the cuticles are not only heavily calcified but also lack any evidence of microfibrils or parabolic structures. A heavily calcified cuticle lacking parabolic structures is contrary to that of the typical, generalized arthropod cuticle.

ON the basis of a broad study of both exoskeletal microstructure and composition, Teigler and Towe (1975) concluded that the trilobite cuticle does not compare as favourably with the generalized arthropod cuticle as had been thought. They suggested the calcified ostracod carapace as a better over-all comparison. In a recent paper on the cuticle of *Asaphus raniceps* Dalingwater and Miller (1977) have criticized this conclusion extensively. With a view towards clarification, some discussion in rebuttal is necessary.

The main point of contention concerns comparison of the cuticular laminations (laminae, lamellae) in trilobites and in the cuticle of the majority of arthropods living today. Two major questions may be addressed: (1) does the trilobite cuticle always contain laminations, and (2) if so, are these laminations typical of those found in most other arthropods?

At present the answer to the first question is unclear. Dalingwater (1973) observed fine, parallel laminae in nine of the fifteen species he studied but none showing these laminae was figured. Teigler and Towe (1975) reported that only six of the twenty species they studied contained laminations. Examples of both types were figured. Dalingwater and Miller (1977) now report that in all nine of their trilobite species some laminae were seen, but only those in *Asaphus raniceps* were figured. Normalizing these data for those species reported more than once there are twenty of forty-four species which show evidence of laminations. It appears that some trilobite cuticles contain laminations and others do not. Recognizing that other interpretations are possible Teigler and Towe (1975, pp. 140, 144) noted that 'the presence or absence of lamellae in trilobites may be due to genetic factors or to fossil preservation . . .' and tentatively inferred on the basis of their statistically inadequate data that 'Until further work can be done, a genetic control appears to be the major factor in their distribution'. Dalingwater and Miller (1977) have now suggested that diagenesis and/or specimen preparation are the controlling factors involved. Indeed, in his 1973 report Dalingwater was unable to find distinct laminae in about 100 sections of *Asaphus raniceps* from the lower 'Raniceps' Limestone (Haget, Öland, Sweden), whereas Dalingwater and Miller (1977) have now found distinct laminae in all of their specimens from this same locality and horizon. One must agree with them that the absence of laminae from *Asaphus* cuticle in the first report was most likely due to methods of specimen

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preparation. Whether this holds true for other species presently said to lack laminae remains to be demonstrated. It seems fair to conclude from all of this that while distinct laminations in trilobite cuticle may not always be seen, the controlling factors involved have yet to be firmly established. It is likely that each case will have to be decided on its own merits. At present, then, a tentative answer to the first question is: it is not known for certain whether the trilobite cuticle always contains laminations.

But it is the second question that is the more important: are the laminations, when observed, typical of those found in most other arthropods? Dalingwater and Miller (1977, p. 21) argue that they are, stating: 'The laminae and organization of the cuticle... are considered comparable to those of many extant arthropod cuticles.' Teigler and Towe (1975, p. 144) suggested that they are not, stating: '. . . the absence of parabolic structures (and helical pore canals) indicates that those lamellae that are found are not the same as those normally observed in the typical extant arthropod endocuticle.'

Laminations are obviously not unique to arthropods so their presence alone is insufficient to make valid a close comparison between the trilobite cuticle and that of the typical arthropod. The typical arthropod cuticle has other characteristics which include 'pore canals', parabolic structures, and a general absence of dense calcification with preferred crystallographic orientation. Teigler and Towe (1975) noted that while some trilobites had laminations and some had 'pore canals' *none* had parabolic structure and all with well-preserved cuticle (i.e. not impressions or replacements, etc.) were heavily mineralized with calcite having c-axis preferred orientation. Agreeing that this is unusual, Dalingwater and Miller (1977) have attempted to play down the significance of heavy, preferred calcification noting that, in addition to many ostracods, some cirripedes are also heavily calcified. Yet barnacles are certainly not typical arthropods and the functional significance of a heavily calcified cuticle attributed to the trilobites by those authors is irrelevant to the present problem.

But conceding these points for the moment, we are still left with the parabolic structure so characteristic of the arthropod cuticle. Teigler and Towe were unable to find parabolic structure in any of their trilobite preparations. They described and figured it in *both* fossil crab cuticle and fossil crab tubercles but they were unable to find it in either the cuticle or tubercles of *Phacops rana* similarly prepared. *P. rana* was chosen because it had clear laminations and therefore should have had parabolic structures were they present; i.e. diagenetic obliteration cannot be invoked. Earlier (1973, p. 837), Dalingwater himself observed that '... microfibrils were not seen even in the best-preserved material . . .'. Nor did Dalingwater and Miller (1977) report parabolic structure or microfibrils in any of their newly prepared trilobites. Yet Neville and Berg (1971) found parabolic structure in a Jurassic crustacean and Dalingwater (1975*a*) has figured it in some eurypterids. Dalingwater (1975*b*) has, for another purpose, figured it beautifully from *Austropotamobius pallipes*—the very same extant crustacean whose cuticle he and Miller feel most typically resembles that of trilobites!

If the trilobite cuticle is to be accepted as a typically laminate arthropod cuticle then it should show parabolic structure. A reasonable answer to the second question then is: until parabolic structures can be shown in trilobite cuticle the laminations observed are not those of the typical arthropod cuticle. When *this* feature is clearly demonstrated in several taxa then the general conclusion that trilobites have a typical arthropod cuticle will make better sense. Until then, and with all other things presently known considered, 'the trilobite exoskeletal microstructure compares more favorably with that of calcified ostracodes than with the typical, generalized arthropod cuticle' (Teigler and Towe 1975, p. 137).

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A TECHNIQUE FOR ACCURATE RECONSTRUCTION OF INTERNAL STRUCTURES OF MICROMORPHIC FOSSILS

by P. G. BAKER

ABSTRACT. The problems involved in the skewed reconstruction of structures of serially sectioned specimens are discussed. It is concluded that the deficiency of existing models, when applied to micromorphic specimens, lies in the fact that no consideration is given to the need to modify the x co-ordinates in skewed grids. A new, mathematically constructed, skewed model is proposed, which eliminates distortion in the x, y plane.

VARIOUS techniques for reconstruction of structures from serial sections have been used for a number of years, either using traces made on wax or plastic sheets of appropriate thickness (Sollas and Sollas 1913; St. Joseph 1937) or producing simple graphic reconstructions (Muir-Wood 1934; Ovcharenko 1967). The inadequacy of reconstructions of the type made by Muir-Wood was recognized by Ager (1956) who appreciated that the most informative orientation is that which depicts the specimen in a semi-profile position, i.e. rotated slightly and tilted towards the observer. To achieve this effect, Ager used the technique of plotting peel traces on to skewed grids in order to enhance the three-dimensional appearance of the reconstructed structure. Ager noted that even using this technique, some salient features would remain hidden. Westbroek (1967) and Baker (1971, 1972) largely overcame this problem by partially 'exploding' their reconstructions. However, although comment such as 'the amount of skew must of course vary according to the structures it is required to present' (Ager 1963, p. 223) is common in the literature, reconstructions of internal structures based on skewed grids almost always lack precise detail of the way in which the skewness is produced and, undoubtedly, the amount of skew in many published reconstructions has been calculated intuitively. The lack of works specially devoted to the techniques of making reconstructions was noted and to some extent remedied by Kats, Popov, and Tkhorzhevskiy (1973). A fundamental problem, remaining unsolved by Kats *et al.* (1973, fig. 5) model is that rotating and tilting a specimen relative to an observer, produces an apparent foreshortening of the x, y, and z axes (text-fig. 1A–D). In order to maintain the correct geometric perspective of the reconstruction this foreshortening must be incorporated into the reconstruction framework. The inadequacy of the majority of previous models (Ager 1963; Kats *et al.* 1973) is due to the fact that the authors had overlooked the need to modify the ratios of the x, y, and/or z co-ordinates on the skewed grid, the inevitable result of this omission being distortion of the reconstructed specimen (text-fig. 1E, F). Where the specimen is large or the magnification small and where the structure being investigated can be seen in relation to the whole shell this distortion, apart from considerations of an aesthetic nature, is probably of little consequence. However, where the shell and the internal structures

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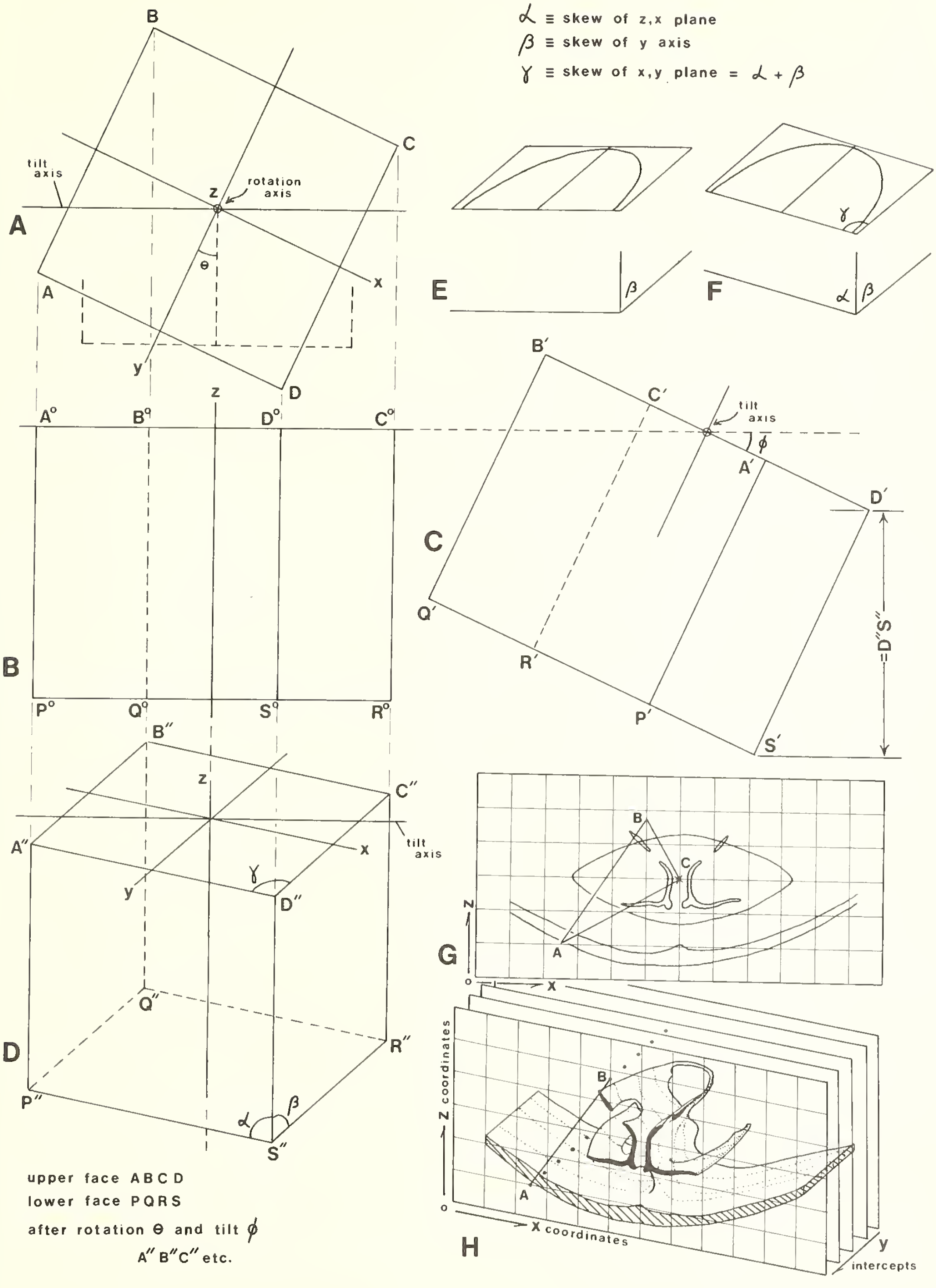
being investigated are very small, microprojection of sections is necessary, at a magnification at which the field of view usually encompasses only part of a structure. In this case the need for accuracy of superimposition of sections becomes critical. A very high degree of accuracy is necessary because it is essential to be able to recognize changes in the relative position of parts of a structure, both with regard to the shell and to each other, through successive sections. It is considered that the deficiency in existing models may be rectified by description of a technique, initially developed (Baker 1972) for the study of early loop development of juvenile zeilleriid brachiopods. The technique described is equally applicable to any micromorphic specimens.

Preparation of the material. In order to determine the internal structure of zeilleriid juveniles selected specimens were mounted at the required orientation in blocks of cold setting resin and serially ground on a parallel grinder at 0·02 mm intervals. Each ground surface was polished, etched, and replicated using cellulose acetate. The techniques used in the production of cellulose acetate peels are now so well known (Kummel and Raup 1963) that it is not considered necessary to describe them further. In view of the need for a very high degree of accuracy of peel superimposition, a technique has been devised in which the inherent error is not likely to exceed 1%. Reference points *A* and *B* are marked on the block with a specially sharpened needle prior to taking the cellulose acetate peels, care being taken to ensure frequent re-marking so that the reference points are not ground away during sectioning.

Superimposition of the microprojected peels. Each peel is mounted, preferably, with one axis of the specimen vertical and the point to be enlarged (*C*) centred in a position (text-fig. 1G) which will ensure its appearance in the field of view at high magnification. The peel is projected on to a squared grid (large enough to accommodate the ultimate magnification) at a magnification (e.g. × 10) which enables the reference points *A* and *B* to be seen. The reference points and the specimen outline (optional) are then drawn in. The reference triangle *ABC* is constructed to locate the position of *C* relative to points *A* and *B* and to fix the orientation of the peel (text-fig. 1G). As the reference points *A* and *B* are incorporated into the peel from the block surface the base-line *AB* must represent a standard reference through successive peels. Therefore, changes in the relative position of features of the sectioned specimen, both with regard to each other and to the reference points, can be ascertained by the changing values of $\angle ACB$.

TEXT-FIG. 1A–D. Graphical reconstruction of a skewed grid based on a cube whose dimensions are 40 mm rotated and tilted through 25°. A, top view after rotation. B, front view of rotated block. C, lateral view of rotated block after tilting. D, observer view of rotated and tilted block. E, F, plot of hypothetical data on rotation and tilt grids to show the high degree of distortion, left and right of the long axis, produced in a reconstruction, E, using unmodified *x* co-ordinates, compared with a reconstruction, F, using skewed *x* co-ordinates. G, plot of preliminary (× 10, linear) and ultimate (× 45, linear) data on to a squared grid to show the establishment of the reference triangle. H, reconstruction of part of an early juvenile *Zeilleria leckenbyi* (Dav.) based on a plot of 'cleared' (× 45) data from five serial cellulose acetate peels obtained from a transversely sectioned shell, showing the form of the posterior part of the frenuliform (bilacunar, Richardson 1975) loop.



α ≡ skew of z,x plane
β ≡ skew of y axis
γ ≡ skew of x,y plane = α + β
A
B
C
D
tilt axis
rotation axis
z
θ
x
y
A
B
C
D
A°
B°
D°
C°
P°
Q°
S°
R°
E
β
F
α
β
γ
B′
C′
A′
D′
Q′
R′
P′
S′
tilt axis
φ
=D″S″
G
H
A″
B″
C″
D″
P″
Q″
R″
S″
γ
α
β
tilt axis
Z
X
o
A
B
C
Z coordinates
X coordinates
y intercepts
upper face ABCD
lower face PQRS
after rotation θ and tilt φ
A″B″C″ etc.

Superimposition of microprojected structures at high magnification in which the reference points are not visible requires that the true position of *A* and *B* relative to the field of view be known.

After the initial procedure described above, the peel is microprojected at the magnification required e.g. × 250, with care being taken not to disturb the specimen's orientation. The microprojected image will be superimposed on the reference axes already constructed on the grid, with the same orientation relative to the reference triangle *ABC* as at × 10, thus locating the points *A* and *B* relative to the enlarged structure but now within the field of view. By recording the z, x co-ordinates 'cleared' data may be transferred to an appropriately skewed grid (text-fig. 1H). Traces of subsequent peels may be accurately superimposed by following the procedure described and then superimposing the skewed grid traces, using the constant base orientation defined by the reference axes (text-fig. 1H). As the reference points are fixed, this technique eliminates the problem of ensuring a constant orientation of the grid relative to the specimen, for successive peel traces.

The skewed reconstruction grid. The skewed grid can be constructed graphically (text-fig. 1A–D). A disadvantage is that it is a laborious process which must be repeated (Tipper 1976) each time the angle of rotation and/or tilt is changed. Ideally, what is required is a rotation and tilt formula which will enable skewed grids, accurate in geometric perspective, to be constructed for any angle of rotation at any angle of tilt of the specimen. Fortunately, such a formula is not difficult to derive. For any model, the amount of skew (α, text-fig. 1D) of the z, x (peel trace plane) co-ordinates may be expressed as $\tan\alpha = \cot\theta/\sin\varphi$ and the amount of skew (β, text-fig. 1D) of the y (trace superimposition) axis relative to the z, x plane, may be expressed as $\tan\beta = \tan\theta/\sin\varphi$ where θ represents the angle of rotation and φ represents the angle of tilt required in the reconstruction. The appropriate amount of foreshortening of the x, y, and z axes may be calculated as follows:

$$\begin{aligned} x \text{ axis} &\equiv \mathrm{P''S''} = \sqrt{\{(\mathrm{AD}\sin\theta\sin\varphi)^2+(\mathrm{AD}\cos\theta)^2\}} \\ y \text{ axis} &\equiv \mathrm{S''R''} = \sqrt{\{\mathrm{DC}\sin\theta\cos\varphi)^2+(\mathrm{DC}\sin\theta)^2\}} \\ z \text{ axis} &\equiv \mathrm{D''S''} = \mathrm{D'S'}\cos\varphi. \end{aligned}$$

Obviously, the initial length of the y axis will be scaled according to the section interval × linear magnification of the microprojected image. The appropriate reconstruction intercepts for y may be calculated using $\mathrm{S''R''}/n$ where $n \equiv$ the number of peels taken from the specimen. For superimposition of horizontal sections, the peel data will be transferred to an x, y grid in which the amount of skew (γ, text-fig. 1D) will be $\gamma = \alpha+\beta$ and the superimposition intercepts will be $\mathrm{D''S''}/n$.

Discussion. Where sufficiently sophisticated computer facilities are available the z, x co-ordinates of each rectangular peel trace can be recorded using a digitizer. This data can then be fed into a computer programmed for 'computerized modeling' (Tipper 1976). Graph plotting facilities would enable a skewed, three-dimensional image to be reconstructed.

A major advantage of the technique is that the x co-ordinates for successive values of z can also be plotted on an x, y (skew γ) grid thereby enabling horizontal reconstructions (Baker 1972, text-fig. 5) to be obtained from transversely sectioned material. Conversely, plotting the x co-ordinates for successive values of y on a z, x (skew α) grid enables transverse reconstructions to be obtained from horizontally sectioned material. Similarly, plotting the z co-ordinates for successive values of x on a z, y (skew β) grid enables longitudinal reconstructions to be obtained. Shading of the reconstruction to enhance the three-dimensional effect is advisable. This may be achieved by line shading or the use of stipple in the manner described by Isham (1963).

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